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Journal canadien des sciences halieutiques et aquatiques

100th Anniversary

100e anniversaire

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The *Canadian Journal of Fisheries and Aquatic Sciences*, previously published as *Contributions to Canadian Biology* 1901–1925, *Contributions to Canadian Biology and Fisheries* 1926–1934, *Journal of the Biological Board of Canada* 1934–1937, and *Journal of the Fisheries Research Board of Canada* 1938–1979, is issued monthly to form annual volumes of 12 numbers plus supplements.

Editorial policy: The Journal publishes original research articles, perspectives (syntheses, critiques, re-evaluations), discussions (comment and reply), and rapid communications. Manuscripts may concern cells, organisms, populations, communities, ecosystems, or processes that affect aquatic systems. They may cover a range of disciplines including biology and ecology of marine and freshwater organisms, limnology, oceanography, physiology, toxicology, genetics, economics, disease, and management. Preference will be given to manuscripts that emphasize understanding of observed phenomena and interpretation of experimental results. The Journal encourages papers that lead from clearly stated purpose or rationale and from testable hypotheses, concepts, or questions to identifiable conclusions or syntheses. Such papers may amplify, modify, question, or redirect accumulated knowledge embodied in contemporary perceptions of a particular state of aquatic sciences. The Journal discourages papers that are essentially descriptive, except in emerging disciplines; have only site-specific or local applications (a certain year, place, taxon, chemical compound, etc.); only confirm previously established principles; or apply standard techniques without breaking new methodological ground.

Manuscripts for publication should be submitted to the Editors, *Canadian Journal of Fisheries and Aquatic Sciences*, Department of Zoology, University of Guelph, Guelph, ON N1G 2W1, Canada (519-824-4120 ext. 2646; fax: 519-767-9798; e-mail: cjfas@uoguelph.ca).

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Publié sans interruption depuis 1901, le *Journal canadien des sciences halieutiques et aquatiques* a paru sous plusieurs titres : *Contributions to Canadian Biology* 1901–1925, *Contributions to Canadian Biology and Fisheries* 1926–1934, *Journal of the Biological Board of Canada* 1934–1937, et *Journal of the Fisheries Research Board of Canada* 1938–1979. Le Journal paraît tous les mois, formant ainsi un volume de 12 numéros, et offre en plus jusqu'à deux suppléments par année.

Politique éditoriale : On publie, dans le Journal, des articles rendant compte de recherche originale, des perspectives (synthèses, critiques et réévaluations), des discussions (commentaires et réponses) et des communications rapides. Les documents peuvent porter sur les cellules, organismes, populations, communautés, écosystèmes ou processus qui affectent les systèmes aquatiques. Ils peuvent relever de divers domaines y compris la biologie et l'écologie des organismes marins et d'eau douce, la limnologie, l'océanographie, la physiologie, la toxicologie, la génétique, l'économie, la pathologie et la gestion. On accorde la préséance aux articles qui contribuent à la compréhension de phénomènes observés et à l'interprétation de résultats expérimentaux. On invite les auteurs à soumettre des articles ayant des objectifs précis ou relevant d'hypothèses, de concepts ou de questions vérifiables et se terminant par de solides conclusions ou d'utiles synthèses. Ces articles enrichissent, changent, mettent en question ou réorientent les connaissances acquises sur divers aspects des sciences aquatiques. On décourage toutefois la soumission d'articles simplement descriptifs (à moins qu'il ne s'agisse de nouvelles disciplines), d'application très limitée (applicables à une seule année, une seule région ou un seul taxon, portant sur un unique composé chimique, etc.); d'articles qui ne font que reprendre les principes énoncés dans des articles précédents; et d'articles rendant compte de l'application de normes sans gain de méthodologie.

Les auteurs voudront adresser leurs **manuscrits** aux directeurs scientifiques, *Journal canadien des sciences halieutiques et aquatiques*, Department of Zoology, University of Guelph, Guelph, ON N1G 2W1, Canada (519-824-4120 poste 2646; télécopieur : 519-767-9798; courriel : cjfas@uoguelph.ca).

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À partir de 1996, tous les numéros de *Journal canadien des sciences halieutiques et aquatiques* sont accessibles sur le Web. On trouvera des renseignements sur les tarifs à <http://www.nrc.ca/cisti/journals>.

EDITORIAL

100th Anniversary of the *Canadian Journal of Fisheries and Aquatic Sciences*

This special edition of the *Canadian Journal of Fisheries and Aquatic Sciences* marks the 100th year in which the Journal has been in print. It has also been available in electronic format since 1996.

The Journal was first published as a multiyear volume (1901–1905) with papers dating between 1900 and 1907, as *Contributions to Canadian Biology*. A new series of volumes with the same name ran from 1922 to 1933. In 1934 its title was changed to *Journal of the Biological Board of Canada* with volumes generally encompassing a 2-year period. In 1938 the title was changed again to *Journal of the Fisheries Research Board of Canada*, which it remained until 1979. A fourth and final title change to *Canadian Journal of Fisheries and Aquatic Sciences* (CJFAS) occurred in 1980. In 1993 editing of the Journal passed to the National Research Council of Canada from the Department of Fisheries and Oceans. The move of the Editorial Office to the University of Guelph in June 1997 completed the transition of editorial responsibility from government to academia. The editors and their years of tenure are listed in Table 1.

The scope of disciplines in the Journal was presaged in the very first volume. It contained reports on fisheries, effects of pollutants on fish, and studies on benthos and plankton. From modest beginnings, the Journal grew rapidly after the 1950s, with the number of pages and papers per year having reached more or less steady state within the last 30 years (Figs. 1*a* and 1*b*). The average length of papers has varied considerably over the years but has stabilized during the last 30 years (Fig. 1*c*). It is encouraging to note that contributors to CJFAS are once again writing as efficiently as they were 100 years ago!

The increase in numbers of papers during the past century has occurred in both fisheries and aquatic sciences. (For the purpose of our census, papers were categorized as having either a central focus on fish, or on other subjects. A small proportion of papers, generally <10%, could not be exclusively assigned to either field.) However, the two disciplines have followed differently variable trajectories (fisheries: Fig. 2*a*; aquatic sciences: Fig. 2*b*). Until the 1930s, more papers on aquatic sciences than on fish were published in the Journal. From the late 1930s to mid-1950s, and again from the mid-1960s to the mid-1970s, the emphasis switched back to fish. However, since the mid-1970s the two fields have been approximately equally represented, with a recent trend back to a higher proportion of papers in aquatic sciences. In sum, these statistics indicate that the change in Journal name to *Canadian Journal of Fisheries and Aquatic Sciences* was therefore fully justified and fully captures the continuing character of the Journal. We shall continue to accept the best manuscripts that come to us whether in fisheries or aquatic sciences.

The epithet "Canadian" is now largely honorary because CJFAS has long been a truly international journal with contributions received from all over the world. However, the Journal has undergone some distinct changes over the years. There has been a progressive change from articles of a more descriptive or site-specific nature to ones of a more analytical and interpretive nature. This change can be noted especially since 1983. The basic scope and policy of the Journal at that time was clearly explained in a statement by the Editors (J. Watson and J.M. Reinhart. 1983. Editorial. Can. J. Fish. Aquat. Sci. **40**(1): 1–2) and restated by us in 1998 (J.C. Roff and M.M. Ferguson. 1998. Editorial. Can. J. Fish. Aquat. Sci. **55**(1): iii–iv). The Journal continues to encourage papers whose emphasis is on concepts, interpretation, and understanding of natural phenomena at all levels of the biological hierarchy in fisheries and aquatic sciences. Contributions that are largely descriptive will normally be entertained only on new themes and in emerging disciplines.

Table 1. The Journal editors from 1901 to present.

Editor	Tenure
E.E. Prince	1901–1921
A.P. Knight	1922–1926
J.P. McMurrich	1927–1933
A.T. Cameron	1934
A.G. Huntsman	1934–1949
W.E. Ricker	1950–1962
J.C. Stevenson	1962–1974
J. Watson	1975–1986
J.M. Reinhart	1987–1988
D.G. Cook	1989–1997
J.C. Roff and M.M. Ferguson	1997–present

Since we have become Editors, we have continued to encourage shorter and more efficiently written papers, and we have set aside some of our annual page allocation for special issues devoted to particular topics. We always welcome enquiries for special volumes dedicated to topics of current interest, however these will always undergo exactly the same peer review process as regular submissions. Other recent changes include the demise of "Reviews" in favour of emphasis on more interpretive "Perspectives," and the new "Rapid Communications." Rapid Communications generally appear

Fig. 1. (*a*) The total number of pages published per year (excluding indices); (*b*) the total number of papers published per year; and (*c*) the average length of a paper, measured in pages, per year.

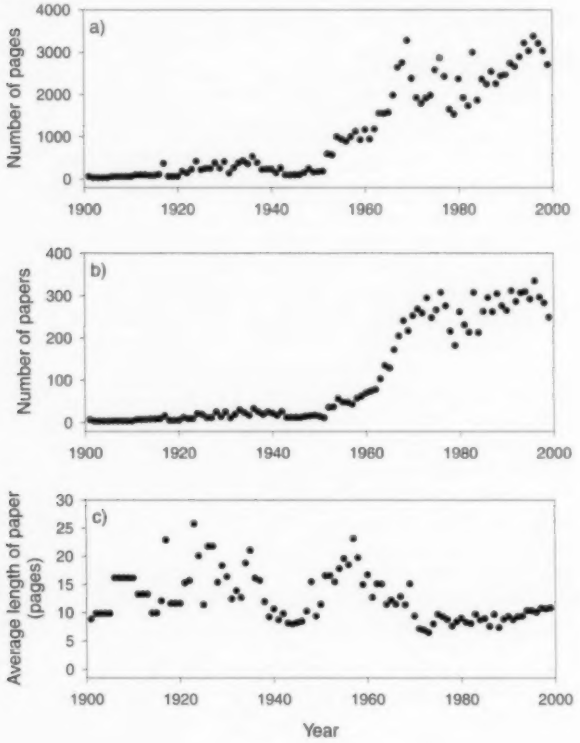
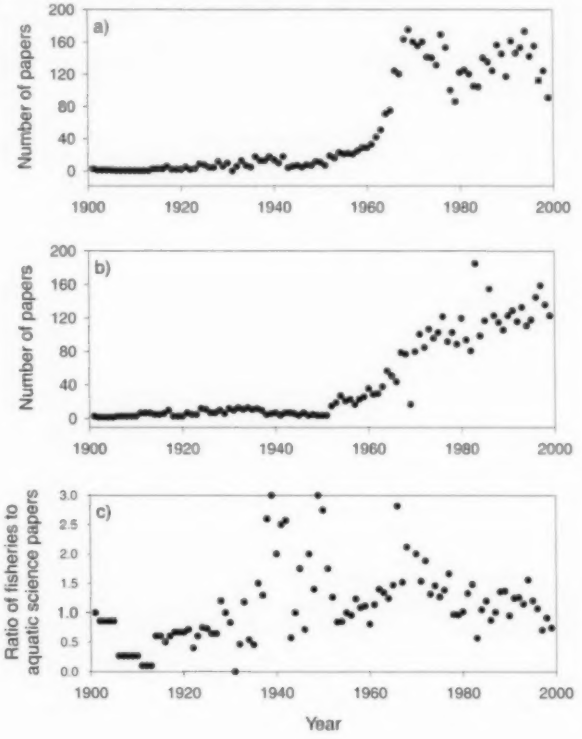


Fig. 2. (*a*) The total number of papers published per year with fish as a central subject; (*b*) the total number of papers published per year with aquatic science as a central subject; and (*c*) the ratio of fish to aquatic science papers per year.



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The present volume contains a series of invited perspectives on an array of issues. These range from older themes reinterpreted with new implications, e.g., stresses on aquatic environments, fish survival and recruitment, theory and models of fishing, conservation and management of aquatic environments and fishes, to newer themes addressing older problems or continuing concerns, e.g., turbulence effects on distributions, ecosystem changes, trophodynamic effects of circulation patterns and fishing practices. Contributions and their implications span the scale from local, through regional to global, and from analytical techniques to prediction in science.

Finally our thanks are to many people who help us to maintain the high scientific and publication standards of the Journal. Our editorial staff in Guelph and Ottawa receive constant and well-deserved praise and thanks from contributors. Our Associate Editors are a constant source of impartial advice and arbitration. Without such assistance our editorial duties would be onerous indeed as we enter our second century of fisheries and aquatic sciences.

J.C. Roff
M.M. Ferguson
The Editors

ÉDITORIAL

100e anniversaire du *Journal canadien des sciences halieutiques et aquatiques*

Ce numéro spécial du *Journal canadien des sciences halieutiques et aquatiques* commémore la 100e année de parution de la revue, qui est depuis 1996 aussi disponible en format électronique.

Le Journal a paru pour la première fois sous la forme d'un volume pluriannuel (1901–1905) contenant des articles écrits de 1900 à 1907; il portait alors le titre de *Contributions to Canadian Biology*. Une nouvelle série de volumes de même titre a aussi été produite de 1922 à 1933. En 1934, le nom de la revue a été changé pour le *Journal of the Biological Board of Canada* et chaque volume couvrait généralement une période de 2 ans. En 1938, la revue est devenue le *Journal of the Fisheries Research Board of Canada* (auquel s'est ajouté, en 1975, le titre français Journal de l'Office des recherches sur les pêcheries du Canada), appellation qu'elle a conservée jusqu'en 1979. Un quatrième et dernier changement de nom a eu lieu en 1980; la revue est désignée depuis lors le *Journal canadien des sciences halieutiques et aquatiques*. En 1993, la responsabilité de la production du Journal a été transférée du Ministère des pêches et des océans au Conseil national de recherches du Canada. Le déménagement du Bureau de la rédaction à l'Université de Guelph, en juin 1997, a complété le transfert de la responsabilité de la direction scientifique du gouvernement vers le monde universitaire. Le tableau 1 présente la liste des Directeurs scientifiques, ainsi que leurs périodes d'exercice.

L'étendue des disciplines que couvrirait le Journal était déjà apparente dès le premier volume; on y trouve des comptes rendus sur les pêches et les effets des polluants sur les poissons, ainsi que des études sur le benthos et le plancton. D'origine modeste, le Journal s'est mis à croître rapidement après les années 1950, puis le nombre de pages et d'articles publiés chaque année s'est plus ou moins stabilisé au cours des 30 dernières années (figures 1*a* et 1*b*). La longueur moyenne d'un article a varié considérablement au cours des ans, mais est demeurée constante au cours des trois dernières décennies (figure 1*c*). Il est encourageant de noter que les auteurs qui contribuent au Journal écrivent de nouveau de manière aussi efficace qu'il y a 100 ans!

L'accroissement du nombre d'articles s'est manifesté tant dans le domaine des sciences halieutiques que dans celui des sciences aquatiques. (Dans notre inventaire, nous avons séparé les articles selon qu'ils traitaient principalement des poissons ou d'autres sujets; un petit nombre d'articles, généralement moins de 10%, ne pouvait être assigné de façon exclusive à l'un ou l'autre domaine.) Cependant, les deux disciplines ont eu des évolutions différentes (sciences halieutiques : figure 2*a*; sciences aquatiques : figure 2*b*). Jusqu'aux années 1930, il y a dans le Journal plus d'articles sur les sciences aquatiques. De la fin des années 1930 jusqu'au milieu des années 1950 et, de nouveau, du milieu des années 1960 jusqu'au milieu des années 1970, l'emphase est plutôt sur les poissons. Cependant, depuis le milieu des années 1970, les deux disciplines sont à peu près également représentées, avec une tendance récente favorisant les sciences aquatiques. Il semble donc, à la lecture de ces statistiques, que le changement de nom pour *Journal canadien des sciences halieutiques et aquatiques* soit vraiment justifié et qu'il rende pleinement compte du caractère continue de la revue. Nous continuerons donc à accepter les meilleurs manuscrits qui nous parviendront dans ces deux disciplines.

L'épithète « canadien » est maintenant devenu dans une large mesure honorifique, puisque le Journal est depuis longtemps une véritable revue internationale qui reçoit des contributions de partout dans le monde. Il y a eu, toutefois, de nets changements au cours des années. On observe une transition progressive, qui s'accentue particulièrement depuis 1983, des articles scientifiques de nature descriptive et d'intérêt local vers les travaux plus analytiques et plus explicatifs. La vision et la politique de la revue ont été clairement énoncées à cette époque par les Directeurs scientifiques (J. Watson et J.M. Reinhart. 1983. Éditorial. J. Can. Sci. Halieutiques Aquat. **40**(1): 1–2) et réaffirmée par nous en 1998 (J.C. Roff et M.M. Ferguson. 1998. Éditorial. J. Can. Sci. Halieutiques Aquat. **55**(1): iii–iv). Nous continuons à solliciter des travaux qui mettent l'emphase sur les concepts, les interprétations et la compréhension des phénomènes biologiques à tous les niveaux de la hiérarchie de la vie dans les domaines des sciences halieutiques et aquatiques. Les études qui ont un caractère surtout descriptif ne seront retenues que si elles

Tableau 1. Les Directeurs scientifiques du Journal depuis 1901.

Directeur	Période d'exercice
E.E. Price	1901–1921
A.P. Knight	1922–1926
J.M. McMurrich	1927–1933
A.T. Cameron	1934
A.G. Huntsman	1934–1949
W.E. Ricker	1950–1962
J.C. Stevenson	1962–1974
J. Watson	1975–1986
J.M. Reinhart	1987–1988
D.G. Cook	1989–1997
J.C. Roff et M.M. Ferguson	1997–aujourd'hui

Figure 1. (*a*) Le nombre total de pages publiées chaque année (à l'exclusion des index), (*b*) le nombre total d'articles publiés chaque année et (*c*) la longueur moyenne d'un article, en pages, au cours des années.

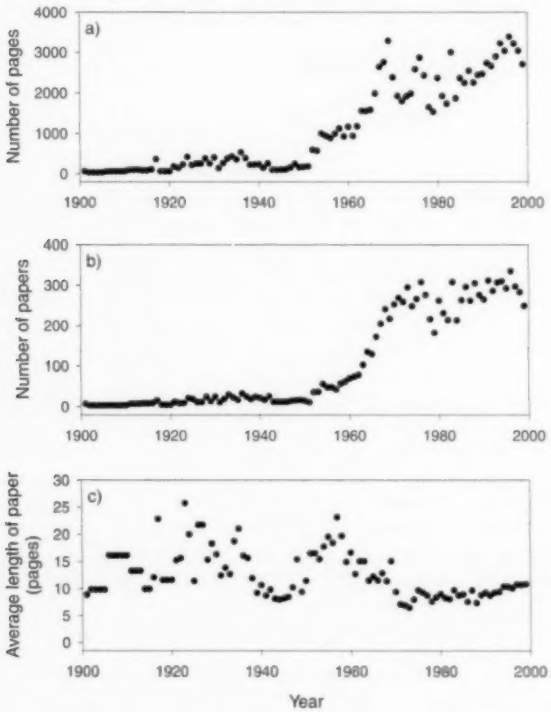
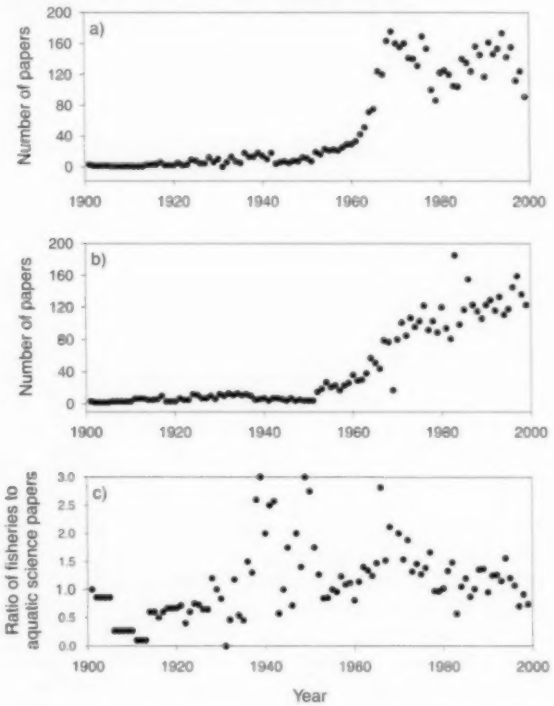


Figure 2. (*a*) Le nombre total d'articles publiés chaque année qui traitent principalement des sciences halieutiques, (*b*) le nombre total d'articles publiés chaque année qui traitent principalement de sciences aquatiques et (*c*) le rapport au cours des années entre le nombre d'articles portant sur les sciences halieutiques et ceux sur les sciences aquatiques.



mettent de l'avant des thèmes nouveaux ou si elles se situent dans des disciplines d'avant garde.

Depuis que nous avons assumé la direction scientifique, nous avons continué à encourager la production d'articles plus courts et écrits de façon plus concise et nous avons réservé une partie de notre espace annuel de publication à des numéros spéciaux dédiés à des sujets particuliers. Nous sommes toujours prêts à discuter de la production éventuelle de numéros spéciaux sur des thèmes d'intérêt courant, mais il est bien entendu que les manuscrits seront toujours soumis au même processus de révision par les pairs que les manuscrits ordinaires. Parmi les changements récents, notons l'abandon de la section « Revues » et son remplacement par une section « Perspectives » qui promeut plus les interprétations, ainsi que l'addition d'une nouvelle section de « Communications rapides » qui sont généralement publiées en moins de 2 mois de leur soumission. Les descriptions des divers types de textes publiés par la revue et les recommandations aux auteurs paraissent dans le premier numéro de chaque année et sont aussi disponibles sur le site Web des Presses scientifiques du Conseil national de la recherche du Canada (www.nrc.ca/cisti/journals/), de même que sur notre site universitaire local (www.uoguelph.ca/~cjfas). Il nous fera toujours plaisir de conseiller les personnes désireuses de soumettre un manuscrit.

Ce numéro spécial contient une série d'articles par des auteurs que nous avons invités à présenter des perspectives sur une variété de sujets. Il s'agit soit de nouvelles interprétations de thèmes plus traditionnels avec des relations inédites, p. ex., les contraintes imposées aux environnements aquatiques, la survie et le recrutement des poissons, la théorie et la modélisation de la pêche, la conservation et l'aménagement des milieux aquatiques et des poissons, soit alors de thèmes nouveaux reliés à de vieux problèmes ou de préoccupations récentes, p. ex., les effets de la turbulence sur les répartitions, les changements dans les écosystèmes, les effets trophodynamiques des patterns de circulation et les méthodes de pêche. Les contributions et leurs répercussions couvrent les échelles géographiques locale, régionale et globale et vont de présentations de techniques analytiques à des prédictions scientifiques.

En terminant, nous voulons remercier les nombreuses personnes qui nous aident à maintenir le haut niveau scientifique et l'excellente qualité de publication du Journal. Le personnel de nos bureaux de Guelph et d'Ottawa reçoit, à juste titre, de nombreux éloges et témoignages de reconnaissance de la part de nos auteurs. Nos directeurs scientifiques associés nous fournissent sans relâche leurs avis impartiaux et participent à l'arbitrage. Sans tout ce soutien, notre travail de direction serait en effet très onéreux, au moment où nous abordons un second siècle de publication dans les domaines des sciences halieutiques et aquatiques.

J.C. Roff
M.M. Ferguson
Les Directeurs scientifiques

Fish habitat modeling: from conceptual framework to functional tools[1]

Daniel Boisclair

Abstract: Natural and anthropogenic perturbations do not always equally affect all parts of an ecosystem, and all parts of an ecosystem do not equally contribute to maintain fish communities. The increasing pressure to use natural resources and to modify habitats led to the development of approaches to identify areas of key importance for fish communities. Following these approaches, aquatic systems could be perceived as puzzles, composed of a multitude of pieces with temporally flexible physical attributes and biological roles. Such a spatially explicit framework requires models that may allow one to predict fish distribution patterns and fish net energy gain once they have adopted a specific distribution pattern. Despite the conceptual appeal of spatially explicit approaches, functional tools may be obtained only after their assumptions have been tested and their models have been validated. Efforts must be deployed to identify temporal and spatial scales at which fish distribution and abundance should be estimated and modeled. Studies on fish behaviour and the energetic consequences of these behaviours must be conducted to insure that bioenergetic criteria used to define fish habitat quality do not depend on arbitrary assumptions about fish activity costs.

Résumé : Les perturbations naturelles et anthropiques n'affectent pas toujours également toutes les parties d'un écosystème et toutes les parties d'un écosystème ne contribuent pas également au maintien des communautés de poissons. La pression grandissante d'utiliser les ressources naturelles ont amené le développement d'approches permettant d'identifier les régions d'une importance clé pour les communautés de poissons. Suivant ces approches, les rivières relativement peu profondes pourraient être perçues comme des mosaïques de parcelles ayant chacune sa valeur énergétique spécifique pour les poissons et les rivières plus profondes et les lacs pourraient ressembler à des sculptures de blocs ayant chacun sa valeur de croissance potentielle pour les poissons. Un cadre de référence spatialement explicite requiert des modèles qui permettent de prédire les patrons de distribution des poissons et le gain énergétique net des poissons une fois qu'ils ont adopté un patron de distribution spécifique. Malgré l'attrait conceptuel des approches spatialement explicites, des outils fonctionnels ne pourront être obtenus qu'une fois leurs prémisses testées et leurs modèles validés. Des efforts doivent être déployés pour identifier les échelles temporelles et spatiales auxquelles la distribution et l'abondance des poissons devraient être estimées et modelisées. Des études sur le comportement des poissons et les conséquences énergétiques de ces comportements doivent être effectuées pour s'assurer que les critères bioénergétiques utilisés pour définir la qualité de l'habitat des poissons ne dépendent pas de prémisses arbitraires au sujet des coûts de l'activité des poissons.

Introduction

Physical, chemical, and biological attributes of lakes and rivers and of the watershed that supplies them with water and nutrients are extremely variable among systems. This situation represents a challenge for ecologists trying to forecast how changes in environmental conditions may affect fish communities. Despite an apparently overwhelming variability in environmental conditions, models have been developed to predict some of the biological properties that we find useful. Contributions of a suite of scientists from Ryder (1965) to Downing et al. (1990) and to Randall et al. (1995) to develop relationships between fish production sensu largo (fish yield, biomass, or production; further referred to as fish production for simplicity) and characteristics of lakes or rivers exemplify, in my mind, what aquatic science is all about: acquiring knowledge that leads to the development of tools that can be manageable and useful for both fundamental and practical purposes.

Current models that attempt to predict the effects of changes in environmental conditions on fish communities generally focus on variables averaged over one or many years and over entire lakes or rivers (e.g., total fish yield or production, seasonal mean biomass, mean chlorophyll *a* concentration, average phosphorus concentration, mean depth, mean flow, total number of degree-days per growing season). However, all natural or anthropogenic perturbations of environmental conditions may not equally affect all parts of an ecosystem. Similarly, all parts of an ecosystem may not equally contribute to the maintenance of fish communities. Furthermore, the impact on fish of any given natural or anthropogenic perturbation may vary with time. Recognition of this situation has led to the development of approaches to locate, enumerate, and evaluate fish habitats and hence to identify areas of key importance for fish communities

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(Bovee 1982; Brandt et al. 1992; Minns and Bakelaar 1999). Such a spatially explicit framework requires models that may allow one to predict fish distribution patterns and fish habitat quality. Despite the conceptual appeal of spatially explicit fish habitat models, functional tools may be obtained only after underlying assumptions have been tested and models have been validated. In this context, my objectives are to (*i*) present attempts to develop methods to estimate and model fish distribution, abundance, and production and (*ii*) discuss problems and solutions related to the use of an energetic criterion, the potential growth under given environmental conditions, to define fish habitat quality. My emphasis on an energetic criterion reflects my own interest in bioenergetics and not a contention about the superiority of this criterion. The capacity of a habitat to provide suitable spawning or overwintering conditions can be expected to give complementary and equally useful information (Cunjak 1988; Knapp and Preisler 1999).

Empirical models of freshwater fish production

Empirical models of freshwater fish production provide indications on the boundaries within which fish communities and aquatic systems may function. The most important conceptual problem of these models may be their potential circularity (phosphorus concentration may affect fish through bottom-up processes, but fish excretion may affect phosphorus availability and primary production: McQueen et al. 1986; Kraft 1992; Vanni 1996). Maybe the use of nutrient loading (D'Arcy and Carignan 1997) instead of nutrient concentration in aquatic systems as a truly "independent" variable could contribute to solving this potential circularity. The most important functional limitation of the empirical models of fish production, which may or may not be related to the conceptual problem, is their confidence intervals that often span an order of magnitude. Most attempts to improve the precision of predictions made by such empirical models have focussed on the selection of potentially more powerful independent variables (for instance, the use by Downing et al. (1990) of primary production instead of the morphoedaphic index to predict fish production). However, estimation of the fish production per se may not be a simple exercise.

Estimation of fish production

Temporal considerations

Most empirical models that try to predict fish production are based on the analysis of results obtained using different sampling strategies and sampling gears. While these differences may contribute to the unexplained variance of empirical relationships, any approach based on the combination of data collected in many lakes is also subjected to an assumption regarding the temporal stability of the systems studied. Sampling designs often require that data (fish abundance and size) be collected in different lakes at different moments. The assumption is made that these data sets are comparable and that the moment of sampling has no effect on the planned comparison. We tested this assumption by assessing the extent of temporal variation in fish abundance estimates within a system, Lake Croche, at the Station de Biologie des Laurentides de l'Université de Montréal. The littoral zone of this lake is of poor quality. Benthic invertebrates are rare, and fish catch using beach seines is low. Hydroacoustic surveys suggest that fish migrate every day from the littoral zone towards the pelagic zone at dusk and back to the littoral zone at dawn (Gauthier and Boisclair 1997). The hypolimnetic zone of Lake Croche (below a depth of 5–6 m) is anoxic during most of the summer, and consequently, vertical migrations do not explain the occurrence of fish in the pelagic zone of this lake at night. This situation led us to believe that many fish from this lake use the lower part of the littoral zone during the day, out of reach of our seines, and migrate towards the pelagic zone at dusk. We estimated the number of fish targets (target strength >52 dB according to Gaudreau and Boisclair 1998) detected by a hydroacoustic system using a horizontal scanning approach. This approach consists of directing the transducer of the hydroacoustic system such that the axis of the acoustic beam is parallel to water surface (Gauthier et al. 1997). Fish targets were subsequently transformed into estimates of fish relative abundance (FRA, fish echoes·100 m^{-3} insonified). During these surveys, hydroacoustic signals were sent from a floating platform set in the pelagic zone of the lake towards the shore. Using this approach, fish cannot be detected within 5–15 m from the shore of Lake Croche because the hydroacoustic beam crosses the slope of the littoral zone before reaching the shore. The isobath where the hydroacoustic beam intersects the littoral is further referred to as the hydroacoustic shore. Sounding was performed at 4-h intervals for 15 consecutive days (Comeau and Boisclair 1998). On most of the sampling dates, the number of targets detected (and hence the number of fish in the pelagic zone) increased at dusk and decreased at dawn with peak FRA at night approximately 10-fold larger than values during the day. Pelagic seining indicated that hybrids of northern redbelly and finescale dace (*Phoxinus oes* × *Phoxinus neogaeus*) were the only planktivorous fish using the pelagic zone of Lake Croche at night (Gauthier and Boisclair 1997). We also noted that maximum FRA at night could vary 12-fold among nights, with the lowest values observed on a night of a full moon (see also Luecke and Wurtsbaugh 1993). Since our study covered only half a moon cycle, we repeated the sampling of Lake Croche to cover two consecutive moon cycles (Gaudreau and Boisclair 2000). On each moon phase (new, first quarter, full, and last quarter), day and night horizontal hydroacoustic surveys were performed over 3 consecutive days spanning from the day before to the day after a specific moon phase. The average number of fish migrating towards the pelagic zone of this lake at night could vary eightfold depending on the moon phase (Fig. 1). These results indicate that in lakes where fish exhibit distribution patterns similar to those found in Lake Croche, the temporal sampling schedules may greatly affect fish abundance, biomass, and production values. Interestingly, the magnitude of the variation that we observed for fish abundance estimates obtained using different temporal sampling schedules is similar to the variation of fish production estimates for a given primary production. This situation suggests that better sampling schedules may contribute to reducing the confidence intervals of empirical models of fish production.

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Fig. 1. FRA at 01:00 in the surface waters of a bay of Lake Croche estimated by hydroacoustic surveys performed using a horizontal scanning approach during two consecutive moon cycles. Solid and opened circles represent the new and full moon phases, respectively. Error bars indicate ±1 SD. Julian days 205 and 235 were not sampled because of storms.

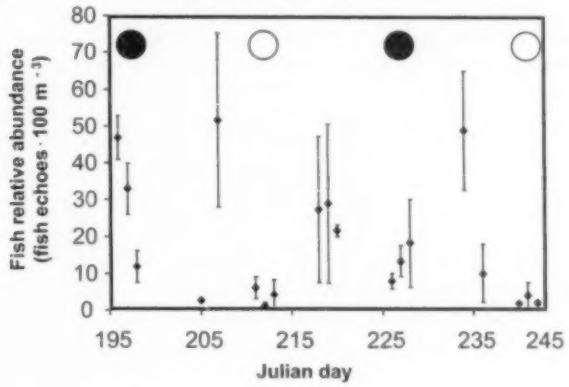
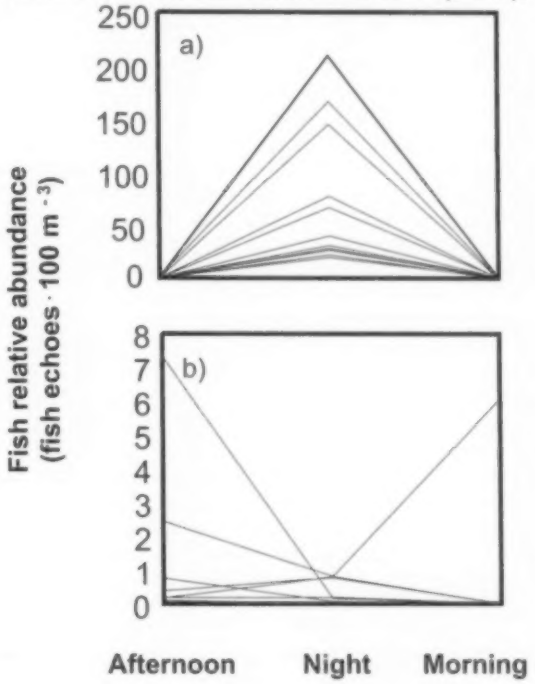


Fig. 2. Daily variations of FRA in the pelagic area of (*a*) Lake Hertel and (*b*) Lake Croche. Each line represents a different 100-m segment of the perimeter of the lakes in which we performed hydroacoustic surveys using the horizontal scanning approach. Distribution patterns of Lakes Cromwell and Silver (not shown) are identical to those of Lakes Hertel and Croche, respectively.



Spatial considerations

Once fish abundance has been evaluated, estimates of fish biomass produced (e.g., kilograms per year) are divided by total lake or river area to obtain production rates (e.g., kilograms per hectare per year). This procedure assumes that the complete area of lakes or rivers contributes to the production of fish or that the exact magnitude of area effectively producing fish has no effect on the biological interpretation of the relationship obtained. High variance of fish density estimates obtained in the littoral zone of lakes and patchiness of fish density values observed in rivers (Duncan and Kubecka 1996; Fischer and Eckman 1997) suggest that not all areas of lakes or rivers contribute equally to fish productivity. This situation may also occur in the pelagic zone of lakes. Gaudreau and Boisclair (1998) performed horizontal scanning of 25–100% of the perimeter of two lakes containing pelagic piscivorous fish, Lake Croche (brook trout (*Salvelinus fontinalis*) and lake trout (*Salvelinus namaycush*)) and Lake Silver (also has brown trout (*Salmo trutta*)), and two lakes lacking this functional group, Lakes Cromwell and Hertel. These lakes are in the Eastern Townships, Montreal, and Laurentians regions of Quebec. Hydroacoustic sampling was performed from a boat located 15–55 m from shore depending on the lake. During sampling, the acoustic beam was directed from a boat towards the closest shore of the lake. Sounding was conducted at 4-h intervals over one 24-h period in each lake. FRA was estimated for 7–12 sequential segments of 100 m of the perimeter of each lake and for two distance classes from the hydroacoustic shore (0–10 m and, when possible, 10–20 m). Average FRA values for any given lake, time of day, and distance from the hydroacoustic shore varied 3- to 84-fold among segments (Fig. 2), supporting the assumption that not all areas of a lake contribute equally to the maintenance of fish communities. Although 1-day sampling does not allow us to determine whether fish consistently use the same segments of the perimeter of the lake (day after day), it is interesting to note that in Lakes Hertel and Cromwell, migration towards the pelagic zone was temporally synchronised among segments (Fig. 2*a*). Peak FRA values, and hence peak migration towards the pelagic zone, occurred at night in all segments. No such temporal synchronism was observed in Lakes Croche and Silver (Fig. 2*b*). These results contrast with the expectation that the presence of pelagic piscivores should induce well-structured fish migrations (Gliwicz and Jachner 1992). The distribution patterns that we observed suggest that the presence of pelagic piscivores may, in fact, induce planktivorous fish to perform feeding migrations that are difficult to predict by their predators. Our data do not permit us to assess the relative effect of the presence of pelagic piscivores and of the sampling design on the presence or absence of temporal synchronism in fish migration. However, our data may be sufficient to suggest that there may be conditions that induce or impede such synchronism. I can only speculate that this synchronism may affect the intensity of predator–prey interactions and the occurrence of nutrient pulses created by fish migrating into the pelagic zone and excreting nutrients (Schindler et al. 1996). While both the occurrence of these nutrient pulses and their effect on the pelagic food web remain to be tested, knowledge that fish may or may not simultaneously migrate towards the pelagic zone may promote new approaches to evaluate the mechanism by which they could affect the pelagic food web.

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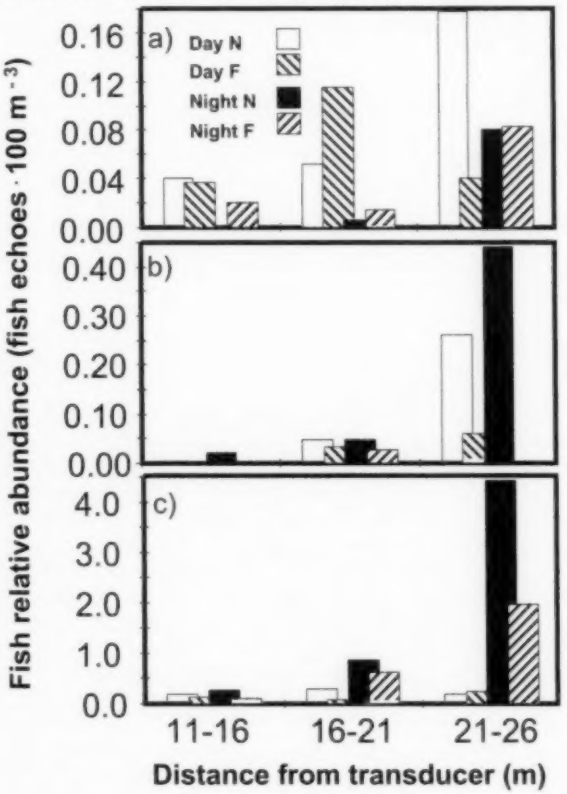
We complemented our evaluation of fish spatial distribution by performing studies to assess variations of fish abundance in the nearshore (approximately 25–40 m from shore) and farshore (approximately 60–75 m from shore) areas of the pelagic zone of three lakes. The complete perimeter of Lakes d'Argent, Cristal, and Orford (Lower Laurentians and Eastern Townships regions of Quebec) was insonified (horizontal scanning) twice at 12:00 and twice at 24:00 on dates within 3 days of the new moon. This strategy was adopted to observe the full magnitude of fish migration and to permit the comparison among lakes (same moon phase). Surveys were performed from a boat cruising approximately 50 m from shore, first with the transducer looking towards the littoral zone of the lakes (nearshore area) and second with the transducer looking towards the centre of the lakes (farshore area). Hydroacoustic recordings were divided into 100-m segments and FRA was estimated for each segment of 100 m in both the nearshore and the farshore areas. FRA was further estimated for three classes of distance from the transducer (11–16, 16–21, and 21–26 m). The volume sampled in each class of distance was calculated independently. On average, FRA increased sevenfold as the distance from the transducer increased (Fig. 3). It is doubtful that acoustic beam spreading over a distance of 15 m may cause such an increase in FRA. One explanation may be that, during horizontal scanning, because the acoustic beam crosses the water surface, hydroacoustic noise caused by even gentle turbulence may increase with the distance from the transducer. Hence, FRAs were analysed independently for each class of distance from the transducer. Nonparametric analyses of variance, using the different 100-m segments sampled at a given time of day as replicates, indicated that the three lakes differed in fish distribution patterns. In Lake Cristal, more fish were observed during the day than during the night (a situation totally opposite of that in Lake Croche), but FRA in the nearshore area did not differ significantly from that in the farshore area (Fig. 3*a*). In Lake Orford, there was no statistically significant difference between FRA obtained during the day and during the night, but significantly more fish were observed in the nearshore area than in the farshore area (Fig. 3*b*). Lake d'Argent also had statistically higher FRA values in the nearshore area, but fish abundance during the night was higher than that during the day (maybe similar to Lake Croche; Fig. 3*c*). These observations suggest that the highest fish abundance in the pelagic zone of lakes does not always occur at night and consequently that data for evaluating fish production or trophic interactions in this zone should be collected using both day and night surveys. More importantly, these data suggest that the degree of coupling between fish distribution patterns and prey distribution patterns may differ among lakes. Zooplankton biomass is generally expected to be highest in the pelagic zone of lakes and to increase at night (Gliwicz 1986; but see Levy 1990). This is also true in our study area (Gauthier and Boisclair 1997; Masson and Pinel-Alloul 1998; Avois et al. 2000). Yet, our data indicate that at least in some lakes, fish abundance is lowest in the pelagic zone when zooplankton is expected to be highest in this area and that fish may not exploit the full extent of the pelagic zone (significantly more fish in the nearshore area than in the farshore area). The lack of coupling between fish and zooplankton distribution patterns

Fig. 3. Day–night variations of mean FRA in the nearshore (N) and farshore (F) areas of the pelagic zone of (*a*) Lake Cristal, (*b*) Lake Orford, and (*c*) Lake d'Argent. The complete perimeters of the lakes were insonified during two consecutive horizontal scanning surveys performed at 50 m from the shore. First, the transducer was directed towards the shore (nearshore estimates), and second, the transducer was directed towards the middle of the lake (farshore estimates). Nearshore and farshore values were divided into three classes of distance from the transducer.



may have the positive effect of providing a refuge for zooplankton that allows a predator and its prey to persist at higher biomass levels (Leslie and Gower 1960), or it may have the negative effect of causing lost opportunities to transfer energy from one trophic level to the next. While the net result of this situation may depend on the balance between the "refuge" and the "lost opportunity" effects, it is tempting to speculate that part of the variance of fish production for a given phosphorus concentration or primary production may be related to the extent of the spatiotemporal coupling between fish and their prey.

Space × time × energy axes

Fish production (Ricker 1975), regardless of the scale of observation, is the product of fish biomass (fish abundance × fish size) and fish growth. However, fish often perform migrations between areas of lakes that differ in environmental conditions at approximately 12-h intervals, and these migration patterns may change from one week to the next. In

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rivers, environmental conditions such as water depth and current velocity may vary on a small spatial scale and, together with water temperature, may differ from one day to the next because of more or less sudden changes of flow produced, for instance, by rain. While it may be possible to estimate fish abundance and size over small spatial and short temporal scales, it is often difficult to estimate fish growth per se on a weekly basis and practically impossible to determine growth on a daily basis. Yet, ecologists are not necessarily destined to try to develop relationships between production rates estimated at some spatiotemporal scales and a composite of environmental variables estimated at all sorts of spatial and temporal scales.

The spatial and temporal heterogeneity of biotic and abiotic conditions should force us to view lakes not as more or less connected littoral, epilimnetic, and hypolimnetic zones but as sculptures of blocks each having a temporally flexible ecological value. Similarly, shallow rivers should be perceived as mosaics of tiles with fluctuating physical and biological attributes. Modeling such spatially and temporally dynamic structures is daunting because it pulls us away from the traditional use of variables averaged spatially and temporally. Furthermore, it represents a conceptual challenge because it requires that we identify the biotic and abiotic variables that affect fish production at the scales selected and that we quantify their effects at these scales. Finally, but not least, this approach constitutes a technical challenge because it requires that we organise and represent the information used as inputs to the model and the predictions themselves in a manageable way. Considering those challenges, I can only recognise the merits of the pioneering work of Brandt et al. (1992) who provided an inspiring example suggesting that it may be feasible, with "spatially explicit models," to integrate bioenergetic models and the spatial structures of physical conditions such as water temperature to estimate potential fish growth in a series of volumes in a lake (Goyke and Brandt 1993; Mason and Brandt 1996). Spatially explicit models focus on among- *and* within-system variations of fish habitat quantity and quality. My conception of the future development of spatially explicit models of fish habitats is based on two questions. How will fish distribute themselves under given sets of environmental conditions? How will fish perform once they have adopted a specified distribution pattern?

Fish distribution

Studies on fish distribution in lakes indicate that fish distribution is heterogeneous (Duncan and Kubecka 1996; Fischer and Eckman 1997; Gaudreau and Boisclair 1998). The development of models to predict fish distribution requires that lakes be sampled according to a standardised temporal and spatial design based on the use of similar gear and assumes that general rules that determine fish distribution exist. While methodological standardisation may be feasible, it does not appear to facilitate the work. Our own studies suggest that sampling during the day and during the night, at different moments of the moon phase, in the littoral, nearshore, and farshore areas of the pelagic zone and, at least in some cases, in the profundal zone of lakes may be required. Nevertheless, when the same sampling protocol is applied in a few lakes (Gaudreau and Boisclair 1998, 2000), results suggest that similarities of fish distribution patterns among lakes may exist (for instance, among Lakes Croche, Silver, and d'Argent or between Lakes Hertel and Cromwell) and that simple variables may be used to explain different distribution patterns (for instance, the presence or absence of pelagic piscivorous fish). Much remains to be done to establish the existence of general rules that define fish distribution patterns. Although this venture appears more than challenging, studies of fish distribution patterns in rivers, to which both engineers and biologists have contributed over decades (Bovee 1982; Leclerc et al. 1994; Whalen and Parrish 1999), suggest that practical and manageable models may be achievable. Recent studies suggest that it may be possible to predict fish distribution in rivers with models based on relatively few variables. For instance, Guay et al. (2000) recorded the water depth, current speed, and substrate diameter in 308 parcels of 1 m^2 occupied by Atlantic salmon (*Salmo salar*) juveniles in a 750-m-long calibration section of the Sainte-Marguerite River (Saguenay region of Quebec). The same physical characteristics were recorded in that section for an equal number of parcels in which no salmon were observed. This data set permitted the development of a multivariate logistic regression that predicts the probability of observing a fish under specified combinations of water depth, current speed, and substrate diameter. This "probabilistic" model was used to predict the spatial distribution of fish in an adjacent section of the same river (validation section, length of 750 m). During this exercise, we produced a map in which the validation section was divided into 10 habitat types (varying from 0 to 1 by intervals of 0.1) defined by the probability of finding a fish according to the probabilistic model (see fig. 5 in Guay et al. 2000). Real fish density (from 0 to 2.5 fish·100 m^{-2}) was estimated in each of these types of habitats by snorkeling the entire validation section. We found a strong relationship between real fish abundance and the predictions made by the probabilistic model (r^2 = 0.81–0.98 depending on water flow). Similar findings were obtained by Boudreau et al. (1996) and Bourgeois et al. (1996) using a slightly different approach. Considering that rivers, because of their dynamic physical attributes related to flow, may represent more challenging habitats to model, I can only presume that similarly efficient models may be developed for lakes. An important contribution of these studies may be that once fish distribution patterns are better understood, the spatial and temporal scales at which we should estimate the interactions between fish and environmental conditions may become clearer.

Fish performance

Yearly or seasonal fish yield and production have often been used as measures of how well fish are doing in lakes and rivers or, alternatively, as a measure of the quality of these habitats. Spatially explicit habitat modeling requires that the currency used to describe fish performance be compatible with the spatial and temporal scales employed for the study of fish distribution patterns. Bioenergetic models may permit us to reconcile the scales used to analyse fish spatial and temporal distribution patterns and to estimate fish performance. The general form of bioenergetic models (also see Winberg 1956; Kitchell et al. 1977) can be written as

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(1) surplus = ingestion – (expenditures + losses)

where "surplus" is the sum of somatic and gonadal growth (surplus energy, sensu Ware 1982), "expenditures" are the costs of performing any metabolic work (standard metabolism, digestion, activity), and "losses" are products released during excretion and egestion (Brett and Groves 1979). The structure of bioenergetic models suggests that surplus energy, which is a valid measure of fish performance, can be predicted for any environmental condition and for any time interval at which fish ingestion, expenditures, and losses can be measured, even if this time interval is too short to estimate surplus energy per se. Equation 1 is fundamentally flawless: "surplus" has to be what is left once "expenditures" and "losses" are subtracted from "ingestion." However, approaches used to transform a theoretical entity into a functional predictive tool are by no means similarly perfect. Bioenergetic models require so much data and pressure to produce predictions is such that data are often replaced by *realistic* assumptions (Ney 1993). In fact, each equation and parameter used to implement bioenergetic models represents an assumption. It may be appropriate to view predictions of eq. 1 as estimates of the net energy gain expected to occur during a specified time interval under given environmental conditions. These predictions are further referred to as expected net energy gain (ENEG).

My work has focussed on two components of fish bioenergetic budgets: the modeling of ingestion and activity rates. Ingestion rate is an obvious choice because it is the fuel for growth. My interest in activity rates stems from research suggesting that this component of fish bioenergetic models may represent a potentially large and variable fraction of energy budgets (Boisclair and Leggett 1989). Hence, improper assumptions about activity rates could severely bias ENEG values predicted by bioenergetic models. Despite the controversy and the criticisms (Hayward 1990; Hewett et al. 1991), the effective role of fish activity rates in bioenergetic models remains unresolved, probably because of the difficulty in estimating this component of the energy budget. One approach employed for that purpose has been to estimate activity rates by difference using eq. 1 (Kerr 1982; Boisclair and Leggett 1989). This approach is amenable only for relatively long temporal scales because it presumes that both ENEG (generally growth) and consumption rates are known. Using this approach, Boisclair and Rasmussen (1996) developed models to predict seasonal activity rates of yellow perch (*Perca flavescens*). They found that 69% of the estimated variation in activity rates could be explained using only fish weight and water transparency as independent variables. Consequently, these analyses suggest that relatively simple models can predict a key bioenergetic component. However, if the objective is to use a traditional statistical framework to predict ENEG using ingestion, expenditures, and losses as independent variables, it is important that these variables be statistically independent. This requirement necessitates the development of approaches to estimate fish activity rates per se.

Methods to estimate fish activity rates per se require three kinds of information: the amount of time that fish spend swimming, the intensity of the movement (generally swimming speed), and models to transform the number and intensity of movements into energy expenditures. Experiments performed in flume respirometers have been used to develop relationships between oxygen consumption, body weight, and swimming speed (Beamish 1978). During these experiments, fish are forced to swim against a current of constant speed and direction. However, it has long been recognised that the costs of swimming at a constant speed and direction may not correspond to those of swimming at the same average speed but with accelerations, decelerations, and turns (Beamish and Dickie 1967). Empirical analyses by Boisclair and Tang (1993) suggested that the energetic costs of spontaneous swimming (including changes of speed and direction) for a given fish weight and average swimming speed may be 6 to 14 times higher than those estimated by forced swimming models. These results supported the hypothesis that accelerations and turns are very expensive and led to experiments to develop models aimed at estimating the spontaneous swimming costs of fish using a more detailed suite of swimming characteristics as independent variables. Over the past 10 years, we have performed 45 respirometry experiments with brook trout ranging from 1 to 42 g wet weight (Krohn and Boisclair 1994; Tang and Boisclair 1995; Tang et al. 2000). During these experiments, fish are free to swim, without any current, in rectangular respirometers (27–108 L) held at water temperatures ranging from 4 to 21°C. Fish swimming characteristics such as the average and the variance of swimming speed, acceleration rates, and turning rates were estimated using the stereocinematographic method (Boisclair 1992*a*). Swimming characteristics varied among experiments such that, for instance, average speed ranged from 3.8 to 16.5 $cm \cdot s^{-1}$. Spontaneous swimming costs ranged from 0.05 to 20.3 mg $O_2 \cdot h^{-1}$. These data permitted the development of models in which fish weight and different swimming characteristics explained 35–91% of the variation in spontaneous swimming costs. More importantly, these experiments confirmed that, for a given fish weight, the energetic costs of spontaneous swimming at a specific average swimming speed are, on average, ninefold higher than the expected costs of forced swimming at the same speed (Fig. 4). Our studies indicate that the use of forced swimming models for fish that change their speed and direction may greatly underestimate the costs of habitat utilisation and overestimate ENEG and habitat value.

The approach that we developed to estimate fish activity rates from videorecordings of their movements allows us to estimate activity rates that are *almost* statistically independent from growth and consumption rates; calculations of both growth and activity rates require estimates of fish weight. By combining this approach with existing models for estimating fish ingestion rates, we have tried to obtain models for predicting fish ingestion and activity rates under small spatial and short temporal scales (Boisclair 1992*b*; Boisclair and Sirois 1993; Sirois and Boisclair 1995; Marchand and Boisclair 1998). So far, we have performed 32 daily experiments with brook trout (0.6–3.5 g wet weight) held in 1- to 8-m^3 enclosures under variable water temperatures (17–21°C) and fish (0.5–3 $fish \cdot m^{-3}$) and zooplankton (0.01–0.29 g $dry \cdot L^{-1}$) densities. Variables such as fish numerical density, water temperature, and fish weight explained 33–82% of the variations of fish ingestion and activity rates (Table 1). While there are arguments to suggest that these

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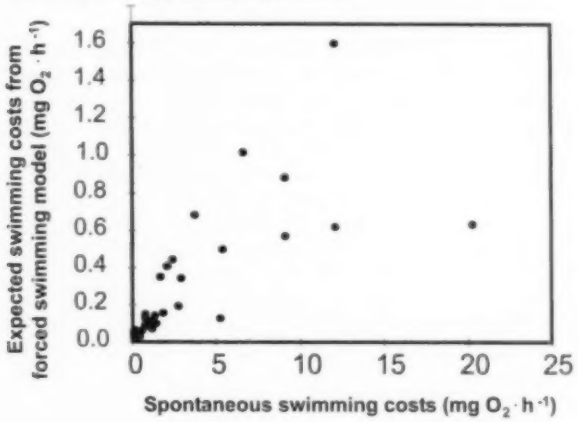
Fig. 4. Relationship between the respiration rates of brook trout predicted by a forced swimming model (Boisclair and Tang 1993) and the observed spontaneous costs of swimming for these fish during 45 respirometry experiments.



experiments may be biologically meaningful (Marchand and Boisclair 1998), the lack of information on the density of fish that is realistic for study in 1- to 8-m^3 enclosures set in lakes makes it difficult to evaluate whether these models have more than a purely academic value. My perspective is that the most important contribution of these findings is that they indicate that it may be possible to develop models for predicting variations of fish bioenergetic components, and hence for predicting ENEG, on relatively small spatial scales and short temporal scales. These characteristics are required to perform spatially explicit modeling.

Modeling ENEG in rivers involves different challenges than that in lakes. One important difference between lakes and rivers is the presence of current, which has direct consequences on the estimation of fish activity rates. In rivers, current speed is expected to increase exponentially from the bottom towards the surface of a river (Dingman 1984). Current speed at any given distance from the bottom may vary within a few seconds (Kirkbride and Ferguson 1995). Hence, the cost of habitat utilisation for fish that constantly remain close to the bottom of rivers may be expected to be adequately described using forced swimming models. However, fish that perform frequent feeding attempts from the bottom towards the surface of rivers may face highly variable current speeds. In such cases, fish movements may involve important changes in swimming speed and direction. While this situation may resemble the definition of spontaneous swimming, in contrast with the experimental conditions used to develop spontaneous swimming models, current is always present in rivers. It could be argued that the cost of swimming at a given average speed (for instance, during a movement towards drifting prey) may be higher in rivers than expected by spontaneous swimming models because movements in a constantly moving and changing environment may require more vigorous and frequent accelerations. The magnitude of the energetic consequences of turbulent currents on fish swimming costs may be expected to depend on the interaction between fish behaviour and current structure. Video observations of the behaviour of Atlantic salmon juveniles suggest that there may be interesting parallels between fish behaviour and current structure (F. Burton and D. Boisclair, unpublished data). For instance, attacks directed by Atlantic salmon juveniles towards drifting prey occur at intervals ranging from a few seconds to a few minutes. The duration of the forward (upstream) phase of attacks, which is expected to be the most energy-demanding part of the attack, ranges from 0.5 to 2 s. Recordings of the structure of water turbulence suggest that significant troughs in current speed (three- to eightfold decrease of current speed) may occur at 5- to 30-s intervals. Furthermore, the duration of such troughs may range from 0.5 to 5 s (Roy et al. 1999). Thus, current troughs may be sufficiently intense, frequent, and long to represent windows of opportunity during which fish could save significant energy. This situation, combined with the presence of eddies (Vogel 1994) creating upstream forces downstream of rocks often used as waiting positions by salmon, may decrease the costs of habitat utilisation estimated using effective fish swimming speed. It can be expected that studies on the behaviour of fish in turbulent currents, the structure of turbulent currents, and the energetics of swimming under such conditions may have a significant effect on estimates of ENEG for fish that live in rivers and on estimates of habitat quality values in rivers.

Table 1. Empirical relationships between specific components of fish bioenergetic models and environmental conditions during 32 daily experiments with brook trout held in enclosures.

I/SMR = 11.31 – 0.33N – 0.47T – 0.48W, R^2 = 0.82
A/SMR = 3.94 – 0.43T + 0.38W, R^2 = 0.33

Note: Growth (G), ingestion (I), and activity (A) rates are presented as multiples of standard metabolic rate (SMR). Independent variables that explained a significant fraction of variations of these bioenergetic components are fish numerical density (N, n·m^{-3}), average fish weight (W, g wet), and water temperature (T, °C).

Epilogue

Empirical models of fish production provide simple and manageable tools that allow us to define general tendencies about the effect of average conditions found in aquatic systems on fish communities. The strength of spatially explicit models resides in their ability to explicitly represent determinant habitats to be protected. In the context of the constantly increasing pressure not only to exploit fish populations but also to alter their habitats both locally and globally, this attribute may not be trivial. The weakness of fish habitat models is the long list of assumptions that affects the validity of their predictions. Testing these assumptions may be the only means to transform a promising conceptual framework into functional tools.

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INVITED PERSPECTIVES AND ARTICLE

Use and abuse of fishery models[1]

Jon T. Schnute and Laura J. Richards

Abstract: Recent failures of important fish stocks give mathematical models a poor reputation as tools for fishery management. This paper examines the role of models in fish stock assessment and identifies reasons why they can fail. Starting with laws of arithmetic, models attempt to relate observed data to unknown quantities, such as the stock biomass and abundance. Typically, the number of unknowns greatly exceeds the number of observations, and models must impose hypothetical constraints to give useful estimates. We use the word "fishmetic" (rhymes with arithmetic) to represent uncertainty in the conversion of arithmetic to practical fishery models. Arbitrary assumptions cannot be avoided, even though different choices can greatly influence the outcome of the analysis. We compare the modeling process in fisheries with that in other sciences. World literature also offers useful analogies. Potential reasons for failure suggest possible improvements to the application of fishery models. We recommend that modelers remain skeptical, expand their knowledge base, apply common sense, and implement robust strategies for fishery management. Particularly creative thought must be applied to the problem of translating scientific knowledge into management practice. Comparisons between fish stocks and financial stocks illustrate some possibilities.

Résumé : L'effondrement récent de stocks importants de poissons a terni la réputation des modèles mathématiques dans la gestion des pêches. Nous examinons ici le rôle des modèles dans l'évaluation des stocks de poissons et déterminons les raisons possibles de leur échec. En partant des lois de l'arithmétique, les modèles tentent d'établir un lien entre les données observées et des quantités inconnues, comme la biomasse du stock et son abondance. De façon générale, le nombre d'inconnues dépasse fortement le nombre des observations, et les modèles doivent imposer des contraintes hypothétiques pour donner des estimations utiles. Nous avons créé le terme « fishmetic » (sur le modèle d'arithmétique, ce qu'on pourrait rendre en français par halieumétique) pour représenter l'incertitude dans la conversion des modèles arithmétiques en modèles de la pratique des pêches. Il est impossible d'échapper aux hypothèses arbitraires, même si des choix différents peuvent avoir une forte influence sur le résultat de l'analyse. Nous comparons le processus de modélisation des pêches avec celui d'autres sciences. La littérature mondiale offre aussi d'autres analogies utiles. Les motifs potentiels d'échec permettent d'envisager des améliorations dans l'application des modèles halieutiques. Nous recommandons aux modélisateurs de cultiver le doute, d'élargir leur base de savoir, d'utiliser leur bon sens et de mettre en oeuvre des stratégies robustes pour la gestion des pêches. Il faut user d'une réflexion particulièrement créative pour aborder le problème de la traduction du savoir scientifique en pratique de gestion. Des comparaisons entre les stocks de poissons et la finance illustrent certaines des possibilités envisagées.

[Traduit par la Rédaction]

Introduction

In the 1990s, mathematical models suffered a declining reputation as tools for fishery management. The collapse of various important fish stocks demonstrated that quantitative stock assessment methods provide no guarantee that a fishery will remain sustainable. Some critics even suggested that mathematical models obscure the truth by narrowing scientific understanding to the realm of quantifiable events. As one fisherman put it (Madill 1998), "Mathematics has highjacked the definition and position of real science."

In this paper, we examine the role of mathematical models in fish stock assessment, and we explain why models can fail. Models act as metaphors of reality. In particular, fishery management deals with poorly understood populations. Any set of concepts describing how these populations respond to fishing and other events can be considered a model. Thus, fishermen, managers, biologists, and the general public all use models, at least implicitly, when they discuss the fate of fish populations. Mathematics can play a useful role by identifying precisely the differences among proposed scenarios. The scenarios can contradict each other, however, and science must reach beyond mathematics for a resolution.

An elegant mathematical model can certainly be alluring to the analyst. Once operational, the model dictates explicit data requirements. On an annual cycle, the model can be

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used to produce abundance estimates and policy recommendations, based on the most recent data. After following this cycle for several years, the analyst may be increasingly convinced that the output correctly represents reality. Like the mythical sculptor Pygmalion, the creator can fall in love with his creation and become blind to other realities.

Modern models have historical roots in the physical sciences, where mathematical assumptions can be applied with high precision. A civil engineer does not reject the science of mechanics because a building collapses. By contrast, models of biological populations have less precise first principles, and the ability to predict stock collapse depends on a broader perspective than a single mathematical model. In this paper, we argue that classical structures for modeling fish populations have a restrictive scope, which must be expanded to include more possibilities.

Fishmetic

Fish populations develop from the arithmetic governed by the fate of individual animals. When a particular fish dies or is caught, the population declines by one unit and the weight of this fish is subtracted from the total biomass. Similarly, when a fish is born, the population and biomass experience corresponding increments, although this calculation depends on a precise definition of birth. Fish growth increases the biomass (but not the population) perhaps by a multiplicative factor. Thus, in a certain sense, the laws of subtraction, addition, and multiplication provide a simple model for the population and biomass trajectories. Similarly, a transaction log of withdrawals, deposits, and interest calculations serves as a numerical model for a bank account.

The inevitable arithmetic of abundance underlies a long history of progressively complex models used to assess fish populations. Most of these have components that account for debits (mortality), credits (recruitment), and interest (growth). Superficially, it might appear that nothing could go wrong with such an approach, which merely captures the transactional arithmetic of a fish population. The analogy with a bank account, however, illustrates some of the potential problems. Deposits might not arrive when anticipated. Withdrawals might be incorrectly recorded or forgotten. Interest rates might change unpredictably. Currency values might fluctuate in response to a broad economy much larger than a single bank account.

The English word "arithmetic" has two pronunciations, where the noun (a-rith′-me-tic) and adjective (a-rith-met′-ic) have accents on different syllables. The word conveys a long intellectual history of exact quantification. To capture the uncertainty of arithmetic in fish population accounting, we propose a new word, "fishmetic," with two similar pronunciations (fish′-me-tic and fish-met′-ic, respectively) for the noun and adjective. The phrases "a model based on fishmetic" and "a model with fishmetic components" illustrate the two possibilities. The new word serves as a reminder that fish numbers may not actually accumulate by the orderly rules of human calculation implied in the model equations.

Modern statistics has invented tools for studying the difference between arithmetic and fishmetic. Model design begins with arithmetic, a set of quantifiable rules defining the modeler's assumptions about fish population dynamics. These typically describe the birth, death, growth, and movement of one or more fish stocks. A computerized version of the model can track the progress of stocks through time while maintaining a record of various theoretical quantities, such as the number of fish and their collective biomass. In modern terminology, these quantities are called *states*, a word with historical connotations from physics. Thus, molecules, satellites, planets, and galaxies can similarly occupy various possible states. A *state space model* (Harvey 1989; Schnute 1994; Schnute et al. 1998) calculates the dynamics of a system as it moves through state space, a name given to the full range of possibilities. For example, a fish population may occupy the state space of biomass values from very small to very large. The model tries to predict where, at a particular time, the population lies along this scale.

A fish population model typically contains many states that can never be observed directly, such as the abundance of fish. Other quantities, derived from the unobserved or hidden states, correspond to actual measurements. For instance, the catch biomass, indices of abundance, and proportions at age theoretically depend on the hidden abundance of the underlying population, structured by age and size. Consequently, such measurable quantities might be used to infer values of the hidden states. More precisely, the model produces scenarios consistent with the rules of population dynamics. Each scenario gives theoretical values for the observed quantities. The scenario that best matches the values actually observed appears to be a reasonable estimate of the true state of nature, including the hidden states. For example, the model might use various observations taken from the fishery and other surveys to estimate the trajectory of stock abundance up to the present time.

The mystery novel offers a metaphor for this process. At one point near the end of the story, the detective dramatizes the crime by going through a scenario that precisely explains all available clues. Everything becomes clear in the light of his explanation. A few observed clues reveal unobserved events. Society takes the right action, based on knowing a hidden state: the identity of the culprit. Similarly, the fishery manager might set the right quota, based on knowing the unobserved stock abundance.

We can develop this analogy further by pointing out that the detective does not merely find clues at random. Mystery literature abounds with examples in which the detective notices details that everyone else had missed. In the story of the horse Silver Blaze (Conan Doyle 1892 (1986, p. 184)), Sherlock Holmes tells the horse's owner about "the curious incident of the dog in the night-time." The owner replies, "The dog did nothing in the night-time." "That was the curious incident," remarks the detective. The story unfolds that the trainer had led the horse from its stable on the fateful night. Only someone known to the dog could have achieved this without causing the dog to bark and "arouse the two lads in the loft." Holmes describes how he concurrently developed scenarios and clues to solve the case. In regard to the dog incident, he points out that "one true inference invariably suggests others."

Fishery models try to unravel hidden secrets of fish stocks, starting with the less romantic science of arithmetic. Inherent defects in the analysis force the modeler to convert from arithmetic to fishmetic. Unlike physics, where mechan-

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ical systems obey precise dynamical laws, fish populations do not experience consistent rates of birth, death, growth, or movement. This difficulty introduces the first element of fishmetic: process error. Furthermore, the observations tend to be highly variable, taken under difficult conditions, leading to the second element: measurement error. In the detective analogy, the scenarios do not hold together very well (process error) and the clues are vague (measurement error). Nevertheless, modern statistics allows process and measurement error to be captured quantitatively as probability distributions. At this stage, fishmetic becomes a synonym for statistics, in which statements of probability replace exact arithmetic calculations. Prevailing theory (Schnute 1994; Gelman et al. 1995; Punt and Hilborn 1997) offers techniques for solving the problem of inferring hidden states from available data, although two schools of thought (Bayesian and frequentist) suggest somewhat different approaches.

This limited definition of fishmetic, however, fails to capture the full range of uncertainty in fish stock analysis. Consider the troublesome case in which a fish stock collapses. What happened to the fish? Three typical explanations are (1) the fishery destroyed the stock, (2) the environment changed so that the stock could not survive, and (3) the fish moved to a different place where they could not be captured. Data showing that the stock declined rapidly may not be adequate to demonstrate which explanation is correct. Starting at the level of arithmetic, three models could be fabricated to represent each scenario. A modeler could overlay each of them with statistics, conduct estimation, and arrive back at the starting point — three possible explanations. This problem illustrates the third element of fishmetic: model uncertainty.

Once again, we turn to literature for an analogy. At the end of his novel *War and Peace*, Tolstoy (1869 (1957, p. 1408)) includes an epilogue that examines history for a possible explanation of human conduct. He illustrates the problem of multiple scenarios with the following simple example. "A locomotive is moving. Someone asks: 'What makes it move?' The peasant answers, 'Tis the devil moves it.' Another man says the locomotive moves because its wheels are going round. A third maintains that the cause of the motion lies in the smoke being carried away by the wind." Tolstoy argues that the peasant's contention is irrefutable. He has a complete explanation that could only be refuted by proving to him that there is no devil. Perhaps another peasant could convince him that "it is not a devil but a German who makes the locomotive go. Only then, because of the contradiction, will they see that they are both wrong." The man who favours the wheels becomes trapped in his own argument. Once he starts his analysis, "he ought to proceed further and explain why the wheels go round." Until he reaches the ultimate cause, the pressure of steam in the boiler, his search cannot stop. The third man recognizes the limitations of the wheel theory, and picks the smoke as his explanation, because it is the "first feature to attract his attention."

Fishery modelers, like scientists generally, understand well the problem of multiple explanations. However, serious statistical analyses similar to those described above require a lot of work. This intense activity can detract from a search for alternatives. It is not easy to work like Sherlock Holmes, building scenarios while accumulating clues. The clues come slowly, with great effort and often at great expense. After all this work, a scientist with a different view may seem like a peasant who blames the devil. In fact, Tolstoy's locomotive scenarios relate rather well with common explanations for stock collapse: (1) the fishery did it — the wheels, an incomplete cause; (2) the environment changed — the devil, an external intervention; (3) the fish moved — the smoke, a convenient theory. Most of the common analytical models are best equipped to deal with explanation 1 because the bookkeeping takes account of removals by catch. But models could readily be designed to revise the bookkeeping in favour of explanation 2 or 3. Thus, the analysis can be tailored to support any desired theory.

Why models fail

In summary, models begin with arithmetic, which must then be qualified by the three elements of fishmetic: process error, measurement error, and model uncertainty. The first two elements can be represented fairly rigorously through the use of probability distributions. Statistical theory then gives estimates of hidden quantities, although often with high uncertainty. The third element, however, introduces a complete unknown, not subject to quantification. Perhaps the proposed arithmetic was wrong in the first place. If so, all bets are off, and the seemingly rigorous statistical analyses have no real meaning.

We have described models in terms of states, some observed (measurements or observations) and others not (unknowns or hidden states). Typically, the number of unknowns exceeds the number of measurements, so that the problem is underdetermined, similar to the problem of constructing a regression line through only one point. Statistical theory applies only in the reverse situation, where the number of observations exceeds (ideally, greatly exceeds) the number of unknowns. Thus, a linear regression problem has three parameters (intercept, slope, and variance) that require at least three observations for estimation. In fishmetic, the indeterminacy problem is resolved by adding structural assumptions that greatly reduce the number of hidden states.

A simple example illustrates this point. Consider a fishery that has operated for 20 years on a population with 10 age-classes. Assume that catch-age data exist for the entire history of the fishery. This scenario gives 200 catch observations, one for each age-class and year. To be useful for inference, each measurement must be predicted from hidden states. In general, catch depends on available biomass and a corresponding fishing mortality. Thus, the 200 catch observations depend theoretically on 200 biomass values and 200 fishing mortalities. The number of unknowns (400) greatly exceeds the number of observations (200). To resolve this problem, two types of constraints are commonly used. First, the modeler assumes dependence among the 200 fishing mortalities; for example, the fishing mortality might be the same on each age-class within a given year. This would reduce the number of independent fishing mortality states from 200 to 20, the number of years. Second, dependencies also exist among the biomass states. For example, various biological processes, combined with fishing, transform the age 4 biomass in year 7 into the age 5 biomass in year 8. Such assumptions reduce the number of independent bio-

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mass states, as long as the biological processes remain stable in time.

Fishery models inevitably require structural assumptions that constrain the unknown states and thus make estimation tractable. These assumptions, however reasonable, remain somewhat arbitrary. Changing them alters the basic arithmetic, with potentially dramatic effects on the conclusions.

Consider a university student taking two courses, one in physics and the other in fisheries. The physics course deals with a spectrum of models to describe paths of falling objects and orbits of planets around suns. Newton's law of gravitation enters the calculations with a constant labeled G_0. The fishery course covers a variety of population models, in which surplus production makes sustainable fisheries possible. Each model has particular data requirements, and many of them contain a constant M to represent natural mortality. The student might come to believe that both courses have similar applications to the real world. When dealing with planets, use one of the physics models. When managing a fishery, apply the appropriate fishery model.

This perceived similarity hides fundamental differences between the two courses. In physics, the models remain applicable across the universe, with no change to the constant G_0. Even a relativistic formulation preserves G_0, which also appears in Einstein's equations as a coefficient of stiffness in the bending of space and time. Fishery models have no such universal application, due to the use of arbitrary assumptions that render models tractable. The so-called constant M certainly differs among species; even for a given stock, M can vary substantially with age and time.

Why do fishery models fail? Perhaps due to misplaced expectations of their value. Clearly, it would be a big mistake to treat them on an equal footing with physical models used to chart planetary orbits. Rather, fishery models serve as useful tools for thought, in which data can be compared with a variety of underlying scenarios. But these scenarios are not unique, and events in the fishery can have multiple explanations, including some not contemplated by the modelers and biologists.

One of us (J.T.S.) began work in this field 25 years ago, after a background in mathematical physics. The computer revolution had begun, and it seemed that computers could handle the relatively straightforward bookkeeping of population biology. It soon became clear, however, that noisy data produce noisy signals. A model acts as a filter, in which a signal emerges from background noise in the data. The definition of noise can fundamentally alter the perceived signal, even if the underlying arithmetic remains the same (Schnute 1987, 1989). State space models, with a clear distinction between measurement and process error, help to clarify the statistical assumptions (Schnute 1994). They also identify the need for imposing constraints on unknown states, as illustrated by the above analysis of a catch-age model. This progression of theory and practice demonstrates that fisheries cannot be modeled by a straightforward analogy with mathematical physics, as might have been naively imagined 25 years ago.

Admittedly, we have somewhat exaggerated the distinction between physics and biology. Physical theory undergoes major revolutions, such as the transition from Newton's theory of gravity to Einstein's general relativity. The former model treats gravity as an attraction between all massive objects, and the latter attributes gravitation to curvature in space–time produced by matter and energy. Weinberg (1992) provides a historical analysis of this transition, in which experimental measurement error plays an important role. He points out (pp. 93–94) that, "There is no theory that is not contradicted by some experiment." Anomalies always occur, and it requires theory to explain which anomalous observations are important.

Furthermore, physical theory does not always have airtight applications. Rockets explode and space probes fail to reach their targets. Such implementations of theory involve millions of physical components. All of these must perform as expected, sometimes in the highly uncertain environment of another planet. As a precautionary measure, designers build redundancy into large physical systems. Similarly, fish populations inhabit uncertain environments, and, in modern terms, fisheries management must take a precautionary approach.

Wilson (1998) analyzes biological systems in the light of modern complexity theory and chaos. In his view (1998, p. 93), "The greatest challenge today, not just in cell biology and ecology but in all of science, is the accurate and complete description of complex systems." Theoretically, a complex system like a fishery results from the interactions of all its components. Thus, understanding such a system requires an extensive knowledge of the underlying facts. For example, much is already known about the constituent parts of cell biology, chemistry, and physics. According to Wilson (1998, p. 99), "Putting a living cell together will be a moon shot, not an Einsteinian revolution of space and time."

Wilson's reductionist view of complex systems sounds a bit like the optimism for model success 25 years ago, and we are not sure that we agree with him. We do, however, agree with his fundamental thesis about the need for facts. Historical fishery models have sometimes restricted data acquisition to the requirements for a particular mode of bookkeeping. Perhaps, like a blind man exploring the elephant, the modeler sees only the trunk or the tail.

Potential remedies

Models are unavoidable tools of fisheries management. Everyone uses models either implicitly or explicitly when they describe the effects of fishing on populations. We have cited examples from fisheries, other fields, and even world literature to identify some of the key reasons why models can fail. Understanding these problems constitutes an important step in identifying solutions. Our discussion below gives four broad categories of potential remedies.

Maintain skepticism

We began this paper with an analogy with the Greek myth of Pygmalion, a sculptor who falls in love with a lifeless statue he created. The analyst must avoid Pygmalion's fate and remain skeptical of the models he creates. Unlike the sculptor's creation, his work may not be blessed by the goddess Aphrodite, who brought the statue to life. Crucial facts may be missing, and no model, however alluring, can completely represent reality. At this stage of their development, fishery models fail to capture many levels of complexity.

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Thus, they serve more as tools for thought than for rigorous analyses of population dynamics. The modeler does well to consider a suite of models, possibly based on different data sources. For example, what would happen if the environment played a major role in regulating abundance? What if fish movement and spatial structure govern the interaction between fish and fishermen? Could species interactions produce effects not noticed when investigating species individually?

To motivate his discovery of general relativity, Einstein proposed a sequence of thought experiments. These mental constructions do not require elaborate mathematics or computer experiments, but they do single out key details of the interaction between an observer and the real world. Similar thought experiments could precede the development of fishery models. For example, we have cited three common explanations for stock collapse. It does not require actual calculation to see that each of them might be consistent with a decline in catch. Further thought might suggest realistic experiments or data sources to distinguish and test these alternatives.

We have analyzed the practical application of fishery models and identified process error, measurement error, and model uncertainty as the three elements of fishmetic. These dictate the need for constraints and arbitrary assumptions, which define scientific limitations of stock assessment models. No discussion can erase this reality. Consequently, the science itself must routinely recognize such limitations and actively consider alternative explanations.

Expand the knowledge base

As Wilson (1998) points out, complex systems cannot be understood without an extensive knowledge of facts. We have cautioned that relevant facts often become confined to the data needed for a particular model formulation. One relatively straightforward extension, called metaanalysis (Quinn and Deriso 1999), uses estimates from a variety of similar populations to give an initial distribution of biological parameters for a particular stock. Essentially, the modeler takes advantage of similar studies elsewhere.

Other extensions go beyond the boundaries of model formulation. What information can be gleaned from oceanographic and climatological studies? Can the analysis be expanded to incorporate interactions with other species, ecosystem characteristics, and comments from fishermen? In some cases, such ancillary data might not be quantitative, but can at least be checked against scenarios developed with a model. In the spirit of thought experiments, what additional biological or survey data might help resolve key model ambiguities?

Richards and Schnute (1998) propose a framework of shared data and analysis as one strategy for advancing stock assessment. Although fisheries cannot be replicated, a long history of shared data from key world fisheries might eventually enable objective scientific development. Suppose, for example, that today's analysts could use credible data from numerous studies that have continued for more than a century (or even a millenium). Surely this long record would reveal truths not apparent from the relatively short time series available for most fisheries. Scientists currently attempt similar exercises for investigating climate change through the use of data from tree rings, ice cores, or ocean sediments.

Apply common sense

We have emphasized that models serve as tools for thought. They can play this role, of course, only if they are well designed and applied. The process begins with exploratory data analysis that allows messages from the data to be revealed with as little imposed structure as possible. For example, Richards et al. (1997) suggest visualization tools for models based on catch-age analysis. We consider it wise to start with simple model structures and add complexity as required or justified by the data. In the spirit of analyses proposed here, various simple alternatives might be considered from the start, so that several model frameworks could be explored concurrently. In this way, the focus remains on the basic thought processes, rather than the details, and the final product can more readily be understood, interpreted, and explained to others.

We envisage models tailored to explicit situations, rather than blind fitting of standard models off the shelf. Classical requirements for quality control never go away. These include residual analyses, diagnostic checking, and verification of computer code. Ideally, team members bring different skills to the analysis, so that the challenge of different viewpoints adds another layer to the diagnostics. We also recognize the need for training. Hilborn and Mangel (1997) give a fresh analysis of the scientific method and illustrate modern techniques for linking data to appropriate models. Hilborn and Walters (1992) and Quinn and Deriso (1999) provide modern references to the theory and practice of fishery modeling.

With advances in theory and computing technology, models can become complex and include a large number of unknown states. In the normal cycle of testing and revision, tweaks in the computer code can be overlooked and programming errors become more probable. During this highly labor-intensive process, modelers can lose sight of central issues and thus forfeit the model's utility as a tool for thought. For this reason, we have emphasized development from simple intuitive structures that capture the main ideas. As models become progressively complex, good practice leads to deeper understanding of the consequences of important assumptions.

Implement robust strategies

Ultimately, fishery models serve to assist a management system, often through a complex social process. The harvest plan and its implementation introduce a final layer of uncertainty. Ideally, the plan should be robust to the full spectrum of uncertainties. Walters and Parma (1996) and Walters (1998) illustrate an analysis of this problem through a regulatory scheme that controls fishing mortality with large spatial and temporal fishery closures. In this way, only a small component of the stock gets exposed to the fishery. Simulation studies show that control of fishing mortality offers a management strategy more robust to uncertainty than direct control of catch. Intuitively, this approach allows the stock to track favourable and unfavourable environmental changes, even when models fail to detect such changes. According to Walters (1998, p. 284), "...the sad fact is that most stock assessment systems are just not up to the task of providing ac-

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curate enough stock size estimates to be safe in the face of fishing technologies that can get the quota even if stock size is much lower than estimated."

These analyses not only propose a sensible concept, but they illustrate the technique for exploring such ideas. Simulations can contemplate many scenarios for fish population dynamics, as well as numerous options for fishery regulation. Regulatory schemes can be evaluated for their ability to meet desired management goals across a wide range of potential realities. Analysts can consider at least two types of decision rules: model based and data based. In the first, an estimation model uses observed data to produce a control value, such as an allowable catch. In the second, the control comes directly from data, such as altering a quota in proportion to a change in an index. Simulation models serve as tools to test the robustness of any regulatory scheme, including rules that combine model-based and data-based controls.

Recognition of model uncertainties has led fishery agencies worldwide to adopt a precautionary approach to management (Richards and Maguire 1998). This approach is now embodied in several international agreements, including (*i*) the United Nations Straddling Fish Stocks and Highly Migratory Fish Stocks Agreement and (*ii*) the FAO Code of Conduct. Both of these require harvest strategies based on stock-specific reference points and predefined decision rules. Such agreements partially follow the example of building codes, where certain standards must be met for plumbing, electrical wiring, and other aspects of construction. Our analysis here shows that fisheries cannot be modeled as precisely as physical systems. Consequently, fisheries require a different approach to setting standards than the construction industry. Although the use of reference points has advanced fishery management, we urge caution in setting them explicitly in relation to one version of the bookkeeping. If the model is wrong, then application of its reference points could be misguided and even deceptive.

Conclusions

In 1931, Gödel discovered a result now considered "a milestone in the history of logic and mathematics" (Nagel and Newman 1958). He used mathematical techniques to show that certain true mathematical statements cannot actually be proved from the axioms of arithmetic. In other words, mathematics contains "undecidable propositions" for which neither a proof nor a counterexample exists. His arguments belong to the field of metamathematics, the mathematical science of investigating mathematics itself. Similarly, in a much simpler fashion, we have used mathematics to articulate the scientific limitations of mathematical fishery models. Because the number of unknown quantities exceeds the number of possible observations, models cannot provide a unique description of underlying events without ad hoc assumptions. This elementary metaanalysis reveals that no fishery model can be completely trusted to capture biological reality.

Although this conclusion seems almost trivial, it is not always highlighted in the literature, theory, and practice of stock assessment models. Furthermore, it is not difficult to extend such metaanalyses in other directions. For example, Wilson et al. (1994) examine a dynamic multispecies model with large chaotic variations in stock size. They conclude that classical single species models cannot track such variations without unrealistic, expensive data requirements. Consequently, they favour entirely different management procedures designed to circumvent this problem.

From a historical perspective, mathematical fishery models have a natural evolution that begins with the attempt to make sense of biological and catch data collected from fisheries. Pieces of the puzzle have accumulated from a diverse literature on growth, mortality, recruitment, and the effects of fishing. By combining these pieces into a unified whole, the scientist obtains a modern fishery model, and this achievement feels like progress. Because the assumptions have strong historical roots, the modeler can easily ignore their role as rather arbitrary constraints and focus instead on the seemingly worthy goal of integrating the known data into a unified whole. Rose (1997, p. 365) claims that "In our haste to free ourselves from descriptive naturalism, we have embraced clever but naïve abstractions of reality, and ultimately, ignorance." He notes that a valid interpretation of data requires the wisdom garnered from direct experience with biology and fisheries. The well-known investor Peter Lynch expresses a similar sentiment in the context of financial management (Lynch and Rothschild 1989 (1990, p. 32)): "It's obvious that studying history and philosophy was much better preparation for the stock market than, say, studying statistics. Investing in stocks is an art, not a science, and people who've been trained to rigidly quantify everything have a big disadvantage."

The shared word "stock" suggests a rather compelling analogy between the worlds of finance and fisheries. Analysts in both fields try to track the dynamics of individual stocks in the context of larger systems, respectively called economies and ecosystems. Managers apply human value judgements to the analysts' results and devise a corresponding plan of action. Potential losses and gains must be evaluated in a framework of risk. Lengthy debates accompany the predictions. Will a rise in the interest rate cause a contraction of the economy and a reduction of stock prices? Will global warming produce an unfavourable climate that reduces the available fish stocks? What technical indicators should be used to decide whether to buy, sell, or hold a financial stock? What reference points provide reliable indicators that the catch should be increased or decreased?

The general public seems to recognize that no model or technical analysis could give a perfect algorithm for managing a financial stock portfolio. Indeed, if such a model existed, everyone would use it, and this collective behaviour would alter the markets and cause the model to fail. Curiously, however, a greater expectation of certainty often accompanies the decisions of fishery managers. Perhaps this stems from the incorrect impression that biological systems follow predictable rules of nature, whereas financial systems depend on unpredictable human behaviour, such as consumer interests and fads. In fact, both systems have elements of predictability and uncertainty that render them fairly comparable. The financial world at least has the advantage of daily stock prices without significant measurement error. Fish stock abundance indices, if available, usually contain high measurement error and correspond to much longer time intervals.

We have used numerous analogies, literary references, and even mathematical arguments to identify the limitations of

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quantitative fishery models. Our scientific analysis implies the need for a new understanding of the role of modeling in fishery management. How should fisheries be managed? We do not have a definitive answer to this question, any more than a financier can give a definitive investment strategy, even though his own philosophy has worked well for a time. Perhaps, by analogy with the view of Peter Lynch, people with a rigid analytical perspective have a big disadvantage in understanding biological systems. This would certainly be true if they trusted their models completely. But a good answer to the problem of fishery management will not come from glossing over the complexities. Even an experienced naturalist might have difficulty assembling the implications of diverse data collected from many places over a long period of time. A well-designed model can greatly assist one's thinking about such a complex data set. The strength of mathematics lies in its ability to reveal the consequences of particular assumptions. Its Achilles heel, however, is that the assumptions might be wrong.

Perhaps the most original thinking needs to go into the process of translating uncertain knowledge into practice. For illustration, imagine a discussion in the spacious boardroom of a mutual fund company as staff members debate the fund's holdings in company X. A technical analyst notes that the stock price has been accelerating upward with good momentum. It might be wise to increase the holdings. A sales analyst believes that consumers will soon lose interest in the product of company X, so it might be okay to hold for a while, but sell when the price rises another 10%. However, an industrial analyst has just learned that the best manager in Company X was hired away by the competitor Y. Her replacement at X, a greenhorn math graduate, will probably require months to understand the marketplace. The team decides to sell all stock in X and invest the proceeds in Y.

Imagine next a similar scene in a much more cramped boardroom at some fishery institute, as the assessment team discusses the prospects for stock X. The modeler notes that the biomass of X appears to be increasing, if anything. The age data hint at a strong new year-class entering the fishery. On the other hand, this might only be an artifact of the data, due to recent sampling difficulties. Probably the quota can be increased by 10%, but in a worst-case scenario, it should be reduced. An oceanographer forecasts an impending El Niño event that could negatively impact the growth and survival of X, so that any anticipated gains might be illusory. Perhaps the quota should remain unchanged. However, an experienced biologist has just returned from an intensive survey of the area occupied by X. The results suggest a major increase in Y, a well-known predator on X, perhaps due to ocean events associated with the coming El Niño. Also, a previously unsurveyed reef appears to be an important rearing habitat for X. The committee decides to establish a protected area around the reef, reduce the quota on X by 10%, but allow an increased bycatch of Y to compensate for the lost biomass of X. A fisherman attending the meeting says that this pretty much agrees with his perception of things, but he does not see that the modeler offered anything useful to the discussion. Furthermore, he has been trying to warn about Y for years, but no one would listen.

These fictitious examples illustrate the flexible thinking that must surround quantitative work in a highly uncertain context. Observations outside the model framework can be highly germane to the issue. Consequently, the discussion should include as many facts as possible. The control options may extend beyond those contemplated by the model. To be useful, models must serve as tools for thought rather than rigid prescriptions. Thus, they must generate strong intuition about system behaviour that contributes to a frank discussion of the options. Contradictory information must be acknowledged and evaluated, and this may not be possible if the model acts only as a prescriptive black box. Although the mathematical formalism can always be extended to include more concepts, it would be naïve to imagine that all available information could be integrated into a single model, particularly when important details may have a qualitative character.

Fisheries take place in a social context. Many factors beyond science govern the outcome of this process. Nevertheless, science can take the larger process into account, at least to some extent. Gathering information from stakeholders during model development enriches the model results and creates an atmosphere for model acceptance. Results with strong intuitive linkages to data are easier to follow and more credible to decision makers, fishermen, and the general public. A modeler not skeptical of his analysis will soon find others who are. Proper use of fishery models comes from a frank recognition of their limitations.

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The cumulative effects of climate warming and other human stresses on Canadian freshwaters in the new millennium[1]

D.W. Schindler

Abstract: Climate warming will adversely affect Canadian water quality and water quantity. The magnitude and timing of river flows and lake levels and water renewal times will change. In many regions, wetlands will disappear and water tables will decline. Habitats for cold stenothermic organisms will be reduced in small lakes. Warmer temperatures will affect fish migrations in some regions. Climate will interact with overexploitation, dams and diversions, habitat destruction, non-native species, and pollution to destroy native freshwater fisheries. Acute water problems in the United States and other parts of the world will threaten Canadian water security. Aquatic communities will be restructured as the result of changes to competition, changing life cycles of many organisms, and the invasions of many non-native species. Decreased water renewal will increase eutrophication and enhance many biogeochemical processes. In poorly buffered lakes and streams, climate warming will exacerbate the effects of acid precipitation. Decreases in dissolved organic carbon caused by climate warming and acidification will cause increased penetration of ultraviolet radiation in freshwaters. Increasing industrial agriculture and human populations will require more sophisticated and costly water and sewage treatment. Increased research and a national water strategy offer the only hope for preventing a freshwater crisis in Canada.

Résumé : Le réchauffement climatique va avoir des effets négatifs sur la quantité et la qualité des ressources en eau du Canada. L'ampleur et le régime temporel de l'écoulement des cours d'eau vont changer, tout comme le niveau des lacs et la période de renouvellement. Dans de nombreuses régions, les milieux humides vont disparaître et le niveau des nappes phréatiques va baisser. L'habitat des organismes sténothermes d'eau froide va se réduire dans les petits lacs. Le relèvement des températures va affecter les migrations des poissons dans certaines régions. Le climat va interagir avec la surexploitation, les barrages et dérivations, la destruction de l'habitat, les espèces introduites et la pollution pour mettre en péril les pêches d'espèces indigènes en eau douce. Les problèmes aigus d'approvisionnement en eau que connaissent les États-Unis et d'autres régions du monde vont menacer la sécurité hydrique du Canada. Les communautés aquatiques seront restructurées suite aux modifications dans la compétition, aux changements dans le cycle vital de nombreux organismes et à l'invasion de nombreuses espèces exotiques. Le ralentissement du renouvellement de l'eau va accroître l'eutrophisation et stimuler de nombreux processus biogéochimiques. Dans les lacs et les cours d'eau à faible capacité tampon, le réchauffement climatique va exacerber les effets des précipitations acides. La diminution du carbone organique dissous causée par le réchauffement climatique et l'acidification va faire croître la pénétration du rayonnement ultraviolet dans les eaux douces. Le développement de l'agriculture industrielle et l'essor démographique vont exiger des techniques de traitement de l'eau et des eaux usées plus perfectionnées et plus coûteuses. L'intensification de la recherche et l'adoption d'une stratégie nationale de l'eau peuvent seules offrir l'espoir de prévenir une crise de l'eau douce au Canada.

[Traduit par la Rédaction]

...by means of water we give life to everything.
Koran 21:30

Introduction

Considering its importance to all life on earth, it is strange that freshwater has been our most mistreated and ignored natural resource. Water has been used as a conduit for diluting and transporting human and industrial waste. These activities were almost unrestricted until the mid-twentieth century and in some areas are little restricted today. Dams, impoundments, and diversions have destroyed river habitats, prevented fish migrations, and mixed the biotas of rivers that have been isolated for many thousands of years. Overexploitation has depleted fish stocks. Airborne pollutants have caused acidification of lakes and contaminated food webs to the point where in many areas, concentrations of pesticides, polychlorinated biphenyls (PCBs), mercury, and other persistent organic chemicals in fishes are high enough to require that human consumption be restricted. Human and livestock wastes have caused the eutrophication of many waters in southern Canada and contaminated them with pathogens that will greatly increase the cost of water treatment and health costs from waterborne illnesses.

Despite these well-known problems, Canadians have a rather cavalier attitude toward aquatic ecosystems, probably

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because water is so abundant. Overall, lakes cover 7.6% of the country's surface, over 755 000 km^2. Canada's rivers discharge 9% of the global flow, 14% of the land surface is covered by wetlands, and 2% is covered by snow and ice (Environment Canada 1998). There are also extensive groundwater reserves in most areas. Globally, only Oceania has such plentiful water supplies.

The abundance of water has also caused Canadians to ignore the effects of climate warming on their water supplies. Research on the effects of climate change on freshwaters is scarce and poorly funded. This is a grave mistake. As I shall show below, in addition to its direct effects, climate warming will exacerbate the effects of many other human activities. The effects of extirpation of fisheries by overexploitation, the deliberate and accidental introductions of non-native species that often displace their native counterparts, the effects of acid rain, increased exposure to ultraviolet (UV) radiation caused by stratospheric ozone depletion, water pollution, and water withdrawals are among the stresses that will be increased by climate warming. Agriculture and forestry will be limited by water shortages. Canadian water abundance, pollutant concentrations, aquatic biota, wetland and riparian areas, agriculture, forests, arctic ice packs, and navigation will be affected. Each stressor viewed by itself does not seem all that harmful (at least to some), but the overall effect will be the degradation of Canadian freshwater on a scale that was not comprehensible to the average Canadian at the end of the twentieth century.

Elsewhere, I have reviewed many of the effects of climate warming on lakes and streams at the Experimental Lakes Area (ELA) (Schindler et al. 1990, 1996*a*) and also on a more general level (Schindler 1997, 1998*a*). Here, I shall focus largely on topics not treated in the above papers, including synergistic interactions, and speculate about the role that climate warming might play in affecting freshwater quality and quantity, fisheries, and other biota in the next 100 years. This topic is enormous, and in the available space, I can give only selected examples of what will happen to make water the most important economic and environmental issue of the twenty-first century.

Effects of global change on water quantity

At present, the amount of water per capita in Canada is huge. But its distribution renders much of it unavailable, for most Canadian rivers flow northward, away from the 300-km-wide band along the U.S. border where almost all of the country's 30 million people reside. Canadians are profligate water users. The average Canadian consumes about 326 L of water per day at home, about twice the per capita water use in Europe (Environment Canada 1998), and many times that of countries in the Middle East (Postel 1998; Falkenmark 1999). This figure does not include industrial, agricultural, or hydroelectric power usages, which would greatly increase estimated water use. Population growth, industrialization, expansion of agriculture, increased demand for hydroelectric power, and other activities will greatly increase the demand for water in the years ahead, both in Canada and globally (Postel 1998).

Effects of climate on water yields from snow and ice fields

Much of the usable water in western Canada originates in the snow and ice fields of the Rocky Mountains. Water from the Rockies feeds rivers that flow to all Canadian oceans: to the Pacific via the Fraser and the Columbia rivers, to the Arctic via the Peace–Athabasca–Slave–Mackenzie River system, and to the Atlantic via the Saskatchewan–Nelson River system. Arid regions of the prairies are particularly dependent on these snow and ice fields. For example, total river flows to the Saskatchewan River system from the Rocky Mountains are 87% of the flow volume at the river's mouth (Schindler and Pacas 1996). Already, agriculture in southern Alberta and Saskatchewan depends heavily on irrigation, and water shortages are sometimes encountered. The glaciers of the Rockies are both receding and thinning. For example, the Athabasca Glacier, a popular tourist stop in the national parks of the Rockies, receded over 1.5 km in the twentieth century. Its losses of ice are over 16×10^6 m^3 greater than is replaced each year (Canadian Heritage Rivers Board 1998). Further recessions of mountain glaciers may jeopardize prairie water supplies.

Effects of increased evaporation on water availability

Most global climate models do not predict great changes in precipitation for Canada. This tends to make people believe that there will be little effect on water availability. However, evaporation increases rapidly as climate warms. Effects are larger than most expect. For example, an increase in average air temperature from 14 to 16°C at ELA caused an increase in evaporation of 30%. As a result of lower precipitation and increased evaporation, permanent first-order streams became ephemeral (Schindler et al. 1996*a*). Lower humidity and greater wind velocity also enhance evaporation, the latter at an exponential rate. Stronger winds have already been observed at the ELA (Schindler et al. 1990), possibly as the result of increased convection over clearcut and burned catchments in the region. However, increased extreme weather events have also been predicted by global climate models (Intergovernmental Panel on Climate Change 1996). Greatly increased evapotranspiration in the catchment of the Great Lakes is expected, despite predicted increases in precipitation for some parts of it (Mortsch and Quinn 1996). Large effects on navigation in the lakes are expected. In brief, only areas that have greatly increased precipitation will escape the effects of drought.

Lessons from the past

Examples from the warm, dry mid-Holocene warn us of impending water scarcity on the prairies. Current global climate models predict that warming in the twenty-first century will cause temperatures to greatly exceed those of the mid-Holocene, when temperatures were only 1–2°C warmer than in the mid-twentieth century.

Lake Manitoba, one of the prairies' great lakes, was dry during the mid-Holocene, as shown by layers of prairie grasses embedded in lake sediments (Teller and Last 1982). Even the droughts of the mid-1930s have important messages for us to consider (Rosenzweig and Hillel 1993). Lakes that were previously exorheic became endorheic, and endorheic lakes either dried up altogether or became much more saline. Chemical composition changes greatly as con-

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centrations increase to exceed the solubility of some salts. Typical calcium bicarbonate waters can become dominated by sodium sulfate or other cation–anion combinations, depending on local geology (Rawson and Moore 1944). Eventually, sodium chloride becomes dominant as less soluble salts precipitate. Few organisms are able to tolerate the highest levels of salinity. Unfortunately, there is no record of changes in the biota of shallow prairie lakes before the "dirty 30s." However, paleoecological studies show that in shallow prairie lakes, there were considerable changes to algae, macrophytes, and other aquatic organisms during the period of low lake levels in the 1920s and 1930s (Vinebrooke et al. 1998; Leavitt et al. 1999).

The special vulnerability of wetlands

There were few, if any, wetlands in the southern prairies in the dry mid-Holocene. Dated peat deposits show that most contemporary wetlands in the area were only formed 3000–4000 years ago (Zoltai and Vitt 1990).

Recent data also indicate that wetlands may be particularly vulnerable. Climate warming exacerbated the effects of Bennett Dam on the Peace River on the vast Peace–Athabasca Delta by contributing to thinner ice cover and weaker spring flows, greatly decreasing the incidence of ice jams that caused spring floods to rejuvenate ecosystems of the Delta (Prowse and Demuth 1996). As a result, shallow, perched lakes in the Delta that are dependent on periodic inundation have disappeared, leading to the demise of important muskrat populations and fisheries. The local economy of the region, which depended heavily on muskrat trapping and country foods, has collapsed (Green 1992; Scrimgeour et al. 1994). Poiani et al. (1996) have shown that increased drought and warm temperatures greatly change the vegetation of prairie wetlands. As expected, during periods when ephemeral wetlands are dry, waterfowl production is greatly decreased (Larson 1994) and acts synergistically with other human activities, as I shall discuss later. The decreased water levels expected in the Great Lakes will cause extensive detrimental effects to wetlands surrounding the lakes (Mortsch and Quinn 1996).

Changes to river and stream flow patterns

Most Canadian streams and rivers outside the mountains have an annual maximum flow in the spring, as the result of spring snowmelt. Typically, from 25 to 50% of total annual flow occurs as winter snowpacks melt. These spring melt pulses typically govern the form of river channels, which are generally shaped by maximum flows (Newbury and Gaboury 1993). Also, the spring floods rejuvenate riparian and floodplain areas, where many plant and animal species depend on periodic inundation (Rood and Mahoney 1990; Green 1992; Schindler 1998*b*). In areas where less precipitation falls as snow, or periodic melting decreases the size of the spring snowpack, many physical and biological features will change with a warmer climate.

Effects of international water shortages on Canadian water security

The growth of human populations, industries, and climate warming will act in concert to increase the demand for water, both in Canada and elsewhere. Water shortages elsewhere may pose further threats to Canadian water supplies, for there are sure to be demands that we share our abundant waters with water-poor regions. Barlow (1999) warned that water is rapidly becoming "blue gold." Much of the Middle East already has so little water that it is reliant on other regions for almost all of its agricultural needs (Postel 1998; Falkenmark 1999). The burgeoning populations and profligate lifestyles of the American Southwest are already causing most of their rivers and aquifers to be oversubscribed. The mighty Colorado River has been reduced to a trickle by the time it reaches the Gulf of California by demands for irrigation water and urban water supplies. The Oglala aquifer, which serves much of the west-central regions of the United States, is being exploited eightfold faster than its waters are renewed from natural sources (Barlow 1999). These conditions will become worse as climate warms, and the demand for Canadian water will increase.

Pressures to export water will come from both inside and outside of Canada. Many believe that Canadians are morally obligated to share their water with the rest of the world, regardless of how wasteful other societies have been with their water supplies or what the effects might be on Canadian water supplies, climate, and aquatic biota. Others simply wish to profit from exports of Canadian freshwater. At present, several cases are in the courts, with multinational corporations claiming that the North American Free Trade Agreement (NAFTA) gives them the right to export Canadian water: a scenario that the Mulroney government assured Canadians could never happen under NAFTA. Until the outcomes of these disputes are clear, we must regard water export as a further threat to Canadian water security.

If the proponents of water export win, water will be exported from Canada to water-poor regions by tankers, pipelines, and rerouting of rivers. Some of the proposed schemes are enormous. The Great Recycling and Northern Development (GRAND) canal scheme would dam James Bay, making it into a freshwater reservoir to store the water entering it from the 20 or so rivers that surround it. A massive series of canals, locks, power plants, and dams would divert the water to Georgian Bay, where it would be flushed through the Great Lakes to feed pipelines to the southwestern United States (Bocking 1987; Barlow 1999).

The North American Water and Power Alliance (NAWAPA) project would be still larger. The Yukon, Liard, and Peace rivers would be diverted to the Rocky Mountain Trench, creating an 800-km-long reservoir that would transport water from the Yukon to Washington State, where it would be supplied to 35 states. The total discharge volume would approximately equal that of the St. Lawrence River (Barlow 1999). Huge fleets of supertankers would operate around the clock to move Canadian freshwater around the world, hauling trillions of litres each year. All of this activity would require the increased burning of fossil fuel, further exacerbating greenhouse warming.

Effects of global change on water quality

As flows decline, the capacity of freshwaters to tolerate pollutant loads is reduced. It is well known that water inputs

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are as important in determining the concentrations and fates of pollutants in lakes and rivers as the "loading" of pollutants (Vollenweider 1969; Dillon and Rigler 1974; Schindler et al. 1978). For biologically conservative chemicals, incoming effluents are simply diluted less. For biologically reactive pollutants, the higher concentrations of inputs and slower water renewal rates will exacerbate eutrophication.

Declining water flows will cause declining inputs of chemicals to lakes from their catchments. For example, in the dry 1970s and 1980s, Lake 239 had declining inputs of all chemicals (Schindler et al. 1996*a*). But lower water flows also cause declines in chemical outputs from lakes, i.e., longer residence times. As a result, for biologically conservative chemicals that enter lakes directly from the atmosphere, sediments, or effluent pipes, the increased water residence times of lakes cause concentrations to increase. For example, sediments are an important source of calcium to ELA lakes (Schiff and Anderson 1987). During periods of drought, calcium increases as a direct function of water renewal time (Schindler et al. 1996*a*). In contrast, biologically active chemicals can decrease because increased residence times allow more time for biological action. Examples include nutrients, as mentioned above, and sulfate, where removal by sulfate reduction is a function of contact time between water and sediments (Baker et al. 1986; Kelly et al. 1987). As the result of increasing calcium inputs from sediments and increased reduction of sulfate followed by sedimentation, alkalinity of Canadian Shield lakes appears to increase as water flows decline (Schindler et al. 1996*a*). The situation is more complicated for seepage lakes, as discussed below (Webster et al. 1996). In summary, few, if any, ions are unaffected by changes in inputs, outputs, or soil processes, causing significant changes to lake chemistry (Schindler et al. 1996*a*). The direction, magnitude, and speed of change in the chemistry of lakes will therefore depend on basin size, morphometry, and water regime, as well as the extent of wetlands in the basin, groundwater flows, and many other features.

Changes in dissolved organic carbon (DOC) are perhaps one of the most important effects of climate warming. Allochthonous DOC is the most important determinant of thermocline depth in small boreal lakes (Perez-Fuentetaja et al. 1999). In small lakes where colored allochthonous DOC inputs are decreased as the result of decreased stream flows, drier soils, and lower water tables in wetlands, waters become clearer, and the increased penetration of solar radiation causes thermoclines to deepen. The effect will be amplified by increased bacterial action and chemical precipitation, as expected with longer water residence times, as well as higher solar radiation due to decreased cloud cover (Schindler et al. 1996*a*; Donahue et al. 1998; Myneni et al. 1999).

However, other studies have documented the formation of shallower thermoclines in warm years, due to rapid onset of spring stratification (Robertson and Ragotzkie 1990; Snucins and Gunn 2000). Climate models indicate that spring will be the period of most intense warming, so that such effects are to be expected. However, the deepening thermoclines at ELA occurred during a period when rapid spring warming was recorded, suggesting that where both factors are present, decreases in colored DOC may be the overriding factor.

Deeper thermoclines and euphotic zones and greater visibility for sight-dependent predators will probably result from the above changes. Thermal capacity also increases, as the result of deeper thermoclines, warmer waters, and generally longer ice-free seasons.

Effects on the quality of drinking water

As flows decline and human populations increase, the quality of water for drinking will deteriorate. Rapidly expanding industrial agriculture will greatly exacerbate the problem, for many industrial farms now put out amounts of nutrients and pathogens that would equal those of a moderate to large city. In many areas, lax municipal or provincial regulations permit effluents from livestock operations with tens of thousands of animals to be released to the environment with little or no treatment. Soil erosion, destruction of riparian areas and wetlands, and overuse of fertilizers are also common in agricultural areas. For example, in central and southern Alberta, most streams, dugouts, and irrigation canals in agricultural areas are out of compliance with provincial guidelines for nutrients and coliform bacteria (Canada–Alberta Environmentally Sustainable Agriculture Water Quality Committee 1998).

In part, the problem seems to be one of increasing virulence of pathogens that have been in water for years. For example, the recently appearing virulent strain 0157 of the common intestinal bacterium *Escherichia coli* is now a widespread contaminant in meat, water, and vegetables in areas where livestock are abundant. The recent tragedy at Walkerton, Ontario, where several deaths have been caused by *E. coli* contamination, demonstrates the potentially great health costs of inadequate protection of watercourses from contamination.

Many citizens believe that the use of more chlorination will solve the problem of providing good drinking water. But there is emerging evidence that the byproducts of disinfection with chlorine can cause a variety of adverse health effects, including bladder cancer (Mills et al. 1998) and developmental abnormalities (Reif et al. 1996; Magnus et al. 1999). *Cryptosporidium parvum*, which has caused gastrointestinal problems worldwide, is resistant to chlorination. Other toxic algae, such as *Microcystis*, can produce microcystin, a potent hepatotoxin (Lambert et al. 1994). At best, the cost of potable drinking water will increase rapidly. At worst, there will be increasing health problems associated with pathogenic bacteria and toxic algal blooms. Only comprehensive approaches to the conservation and management of the catchments that supply drinking water can prevent major water problems.

Effects on fisheries

Warming has direct effects on fisheries as well as amplifying the effects of other human and natural stresses to freshwater ecosystems. Among direct effects, waters of many large, unstratified northern lakes that currently support cold-water fisheries may warm to above the optimum temperatures for species like lake trout (*Salvelinus namaycush*), lowering the production of desirable species. Even at sublethal temperatures, warming would cause severalfold increases in the energy requirements of young-of-the-year lake trout (McDonald et al. 1996).

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Wind velocities have also increased at ELA (Schindler et al. 1990), and coupled with forest fires and clearcut logging in the area, small lakes are more exposed to wind. This has caused a decrease in the incidence of transient thermoclines in the epilimnions of lakes (M.A. Xenopoulos and D.W. Schindler, unpublished data), as well as contributing to the increasing thermocline depth discussed above (Schindler et al. 1990). The net result of increased thermocline depth is to decrease the subthermocline habitats available as summer refugia for cold-water species. Other studies support the possibility that increases in warmwater species may affect cold-water species like lake trout more than direct thermal stress (Shuter and Meisner 1992).

One study also suggests that some cold stenotherms may adapt to warm temperatures. In three of four lakes investigated at ELA, lake trout showed the usual preference to spend most of their time in hypolimnions less than 15°C. However, one population, in Roddy Lake, remained throughout the summer in the epilimnion at temperatures of 20–21°C (Sellers et al. 1998). This fishery is also more productive than others of the area (K. Mills, Freshwater Institute, Winnipeg, MB R3T 2N6, Canada, personal communication). The frequency of occurrence of such adapted populations is not known, and the above studies need to be backed up with genetic information before the possibility that they are adapted to warmer temperatures can be accepted. In another case, lake trout exhibited behavioral adaptation, spending much of their time near cold springs, with occasional feeding forays into lakes that have temperatures which would normally exceed thermal tolerances (Snucins and Gunn 1995).

Some fish species are expected to simply change their distribution as temperatures warm. In particular, their migrations to colder parts of lakes and streams will be more difficult as water temperatures exceed temperature tolerances or become ephemeral. Streams appear to be particularly vulnerable. For example, Meisner (1990) predicted that increasing temperatures will eliminate habitat for brook trout (*Salvelinus fontinalis*) at the southern end of their range. Similarly, in mountainous regions, the warming of montane regions is predicted to render a high proportion of streams too warm for native fish species, which will retreat to increasingly isolated high-altitude headwaters (Rahel et al. 1996). Eaton and Scheller (1996) studied the temperature tolerances of 57 freshwater species in the United States. They predicted that climate warming caused by a doubling of CO_2 would reduce habitat for cold- and cool-water species by 57%.

Based on modeling studies, Magnuson et al. (1990) suggested that in large lakes, thermal stratification may become stronger and that shallower thermoclines may increase the deep cold-water habitat for fishes. So far, the models have not been verified by data in great lakes, although the predictions are consistent with the results in smaller lakes, as discussed above.

Effects on other biota

Many effects of climate on lower trophic levels have been noticed. Temperature is well known to affect the geographical distribution of various diatom species (Reynolds 1984) as well as affecting the growth rates and competition for nutrients of algal species (Rhee and Gotham 1981). Differential temperature tolerances can affect the outcome of competition between species (Tilman 1982). There is a considerable literature on the temperature ranges preferred by various algal species, but it is too large to review here. Warmer waters also increase the outbreaks of toxic algal blooms and their toxicity to other organisms (Hallegraeff 1993; Gilbert 1996).

Among the zooplankton, feeding, assimilation, growth, and reproduction roughly double for a 10° increase in temperature (Schindler 1968). Maturation is at younger age, and broods are produced more frequently (Orcutt and Porter 1984). Species richness will probably increase (Stemberger et al. 1996). Other community characteristics, such as vertical distribution and competition, will also change, but the topic is too large to discuss here.

Many invertebrate species will complete their life cycles more quickly. For example, Wilhelm (1999) found that *Gammarus lacustris* required 3 years to complete its life cycle in alpine lakes in cold years, but in warmer summers, this could be decreased to 2 years. The same species at lower elevations completes its life cycle in a single year.

In summary, some of the above studies are based on scenarios from global climate models, and predictions remain to be verified. But it seems clear that warming will modify aquatic communities to affect interspecific interactions between predators and prey and warmwater and cold-water species of competitors.

Effects of climate warming on groundwaters

Groundwaters and groundwater-fed lakes are also affected by climate warming. For lakes, the importance of position in the landscape has been documented (Kratz et al. 1997). Lakes high in the landscape tend to have groundwater inputs diminished by drier conditions. In particular, declining inputs of alkalinity via groundwater make the lakes increasingly dominated by acidic inputs from precipitation. The effect can be great enough to delay or prevent the recovery of acidified lakes, even when sulfate inputs are greatly reduced (Webster and Brezonik 1995; Webster et al. 1996). If the precipitation is quite acid, acidification of the lakes can be greatly accelerated (Webster et al. 1990).

In contrast, lakes downstream in the aquifers have increasing inputs of chemicals from groundwater because drought causes increased contact time of groundwaters with substrates (Webster et al. 1990). The direction and magnitude of the effect on water chemistry are predictable from lake order, substrate chemistry, and flow paths, and models of key processes are quite advanced (Riera et al. 2000).

We probably know enough about the factors affecting water chemistry and sediment water interactions that it should be possible to construct models which will accurately predict the rate and magnitude of changes in water quality under various climate change scenarios in lakes with surface inputs, but so far this has not been done.

Synergistic effects of climate change and other stressors

The overall effects of climate and other human stressors are generically referred to as "global change" (e.g., Mungall

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and McLaren 1990). Oddly, despite the recognition over a decade ago that such "cumulative effects" of human activity were occurring, little research has been devoted to such issues. Below, I give some examples of cumulative interactions with climate that may be of significance to Canadian freshwater.

Climate warming and ecological invasions

The invasion of Canadian freshwaters by non-native species is perhaps the greatest threat to the integrity of lakes and rivers. Several general reviews have summarized North American data. Approximately 700 species of fishes occupy temperate North America. Of these, 103 species and subspecies are endangered, 114 are threatened, and 147 deserve special protection (Allan and Flecker 1993). Between 1900 and 1999, 123 freshwater species became extinct in North America (Ricciardi and Rasmussen 1999). Freshwater mussels are even more threatened than fishes. Of 297 species, 13 are already extinct, 40 are endangered, 2 are threatened, and 74 more are candidates for protection in the United States (Ricciardi et al. 1998).

Lodge (1993) speculated that climate warming may help to accelerate the rate of spread of non-native aquatic organisms and the extinction of native species. This certainly appears to be the case for recent invaders to the St. Lawrence – Great Lakes.

The original biotic communities of the Great Lakes are gone forever. The opening of the Welland Canal in 1829 heralded the beginning of the problem with non-native species. The first well-known accidental introduction was the sea lamprey in the 1920s, which devastated lake trout stocks. Following the demise of the lake trout, several non-native salmonids were introduced into the lakes. Today, the Great Lakes are a "fish zoo."

Waves of accidental invertebrate introductions have resulted from discharge of ballast water from Eurasian ports. Among the most notorious invaders were the zebra mussel, *Dreissena polymorpha*, and the large predatory cladoceran *Bythotrephes cederstroemi*. The zebra mussel has all but obliterated native mollusks from many areas of the lakes. It causes millions of dollars in damage from clogged water pipes. Its high filtration rates and great abundance (MacIsaac et al. 1992; MacIsaac 1996) have greatly cleared the waters of the lower Great Lakes, once clouded by algal blooms caused by excessive phosphorus inputs from detergents, sewage, and bad land use practices, reaching the point where some have advocated the return of some of the now partially controlled phosphorus sources to attempt to maintain a food source for native fauna.

Restrictions on ballast water were imposed to counter the continued inputs of foreign biota to the Great Lakes. Tankers from foreign freshwater ports are now required to change their ballast water at sea. Unfortunately, these restrictions have not been successful. When ballast water is changed, about 5% of the original water is retained in the ballast tanks, containing millions of organisms. In addition, there is only about 90% compliance with the requirement for flushing, indicating lax enforcement. The overall result has been that species tolerant of brackish water are now favored, largely from the Ponto-Caspian area that includes the Black, Caspian, and Aral seas. This area accounts for about 75% of recent invaders to the Great Lakes. Ponto-Caspian invaders include fishes and crustaceans, as well as mollusks (Ricciardi and MacIsaac 2000). Non-native species now dominate the Great Lakes, with enormous ecological and economic consequences. The invasions continue, and the lakes have entered a phase that Ricciardi and MacIsaac (2000) termed "ecological meltdown."

What does all of this have to do with climate warming? Firstly, many of the economic advantages once believed to have been conferred by the Welland Canal may be undone if the predicted effects of warming occur. Shipping and navigation in the Great Lakes will be severely curtailed if the predicted decreases in water level occur. Secondly, most of the Ponto-Caspian species originate in warmer waters, which should amplify their competitive advantage over the cold-water species of the Great Lakes as the temperature of waters increases. The replacement of native species with non-native species may also change the biomagnification of contaminants. For example, Mazak et al. (1997) showed that zebra mussels have become an important vector transferring organochlorine contaminants to waterfowl.

Climate warming and human impacts on fisheries

Inland fisheries are also in jeopardy from a variety of factors, of which climate warming is but one. Increased access caused by logging roads, seismic lines, and other "linear disturbances" plus enormous improvements in snowmobiles and all-terrain vehicles make it possible for fishers to ride to remote lakes and streams that were inaccessible by motor vehicle only a decade or two ago. Once at the lake, powerful outboard motors take fishers rapidly to prime fishing spots, where fish are easily located with sonar. The increased ease of exploitation is causing the rapid decline of large carnivorous species. For example, the catch per unit effort of many sport fishes in Alberta has declined precipitously in the past 10 years (Ryerson and Sullivan 1998). Overexploitation by commercial fisheries has already caused the collapse of the fisheries of many large lakes in the province (Mitchell and Prepas 1990). Changes in angling regulations over the past two decades and anecdotal evidence also suggest that depleted freshwater fisheries are already very common in southern Canada.

The poor ability of lake trout to recover following population declines is of particular concern. The lake trout of Lesser Slave Lake did not recover following overexploitation by commercial fisheries in the early twentieth century and have not been seen in this enormous (1160 km^2) lake since the 1940s (Mitchell and Prepas 1990). The population of Lake 223, which was reduced by experimental acidification in the 1970s and 1980s, has not recovered fully, although the lake has returned to normal pH values (Mills et al. 2000).

Destruction of habitats may contribute to the decline in fisheries. Roads and railways often dissect riparian areas and stream channels, cutting off spawning or rearing habitats and migration routes (Mayhood 1992). Erosion causes turbidity and sediment accumulation. When humans dwell along lakes and rivers, they usually remove sunken trees, weeds, and other objects that serve as cover for fishes to make boating and swimming more convenient. The reduction in physical habitat relates directly to changes in fish production (Christensen et al. 1996), as shown by experimental habitat

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manipulation at the ELA (K.H. Mills, Freshwater Institute, Winnipeg, MB R3T 2N6, Canada, personal communication).

Climate warming and the resulting changes in pollutant concentrations, communities, and water exports would all cause further depletion of freshwater fisheries that have already been savaged by overharvesting, destruction of habitat, dams, diversions, introductions of diseases, parasites, nonnative fishes, and pollutant loads.

We can expect the freshwater fishery to collapse much in the manner that cod and salmon fisheries already have. The west coast salmon fishery is already in trouble, despite hundreds of millions of dollars of research and mitigation. The dams on the Columbia River in the United States have totally destroyed the anadromous fishery in the upper reaches of the river, including those in southern British Columbia. The Atlantic salmon has been nearly extirpated from many rivers where the species was once plentiful.

Climate warming and contaminants

Climate warming may affect contaminant distributions in several ways. As surface waters become warmer, the ratio of mercury methylation to demethylation should increase (Ramlal et al. 1993), causing greater contamination of aquatic fauna (Bodaly et al. 1993).

The declines in DOC due to climate warming would allow deeper penetration of UV radiation, as discussed above. This would presumably allow greater conversion of methyl mercury to elemental mercury, the form susceptible to loss to the atmosphere (Sellers et al. 1996). Once in the atmosphere, mercury is susceptible to long-range transport and biomagnification in distant food chains (Schindler 1999).

Many organic contaminants, including PCBs, dioxins, pesticides, and other toxic compounds, are semivolatile, readily reemitted to the atmosphere from contaminated surfaces at higher environmental temperatures, and redeposited at cooler sites. Warmer climate should cause reemission to increase. In contrast, until permanent snowpacks and ice deposits melt, high-latitude and high-altitude catchments, snowpacks, and glaciers would remain as important "sinks" for semivolatile pollutants (Simonich and Hites 1994; Blais et al. 1998). Particularly at high-latitude sites, contaminant levels are already unacceptably high in predators, including indigenous people (Arctic Monitoring and Assessment Programme 1998). It should be noted that mercury has many characteristics in common with organic substances: long-range transport, semivolatility, and lipophilicity. It is not therefore surprising that concentrations of mercury are also high in northern predators and aboriginals (Arctic Monitoring and Assessment Programme 1998; Schindler 1999).

Synergistic effects of climate warming and acid precipitation

In eastern Canada, acidification of rivers has already jeopardized Atlantic salmon. As others and we have shown, climate warming causes further acidification of rivers and some lakes, as sulfur deposits in wetlands and littoral areas of lakes are reoxidized (Bayley et al. 1992; Schindler et al. 1996*a*; Yan et al. 1996). This can be coupled with decreased inputs of base cations as the result of declining stream flows or groundwater inputs, as discussed above, increasing the acidifying effect. On the other hand, in lakes, increased sulfate reduction as water renewal decreases causes increased alkalinity (Schindler et al. 1996*a*).

Climate warming, acid precipitation, and stratospheric ozone depletion: a triple whammy

Above, I have discussed the increased transparency of lakes as the result of decreased DOC inputs and increased removal by precipitation and bleaching. The effect is most pronounced in acidified lakes, where the effects of increasing incident UV-B are amplified manyfold by greater penetration of solar radiation (Schindler et al. 1996*b*; Yan et al. 1996; Donahue et al. 1998). Indeed, increased penetration of shortwave solar radiation may cause increased conversion of methyl mercury to elemental mercury, which is then released to the atmosphere (Sellers et al. 1996). The effects of UV on other chemical cycles have scarcely been studied.

Canadian research on freshwater problems: from best in the world to down the drain?

In the mid-1960s, many aquatic scientists, myself included, immigrated to Canada because of new and exciting approaches to water research. Large freshwater laboratories were formed by the federal government, including the Freshwater Institute in Winnipeg, Manitoba, the Canada Centre for Inland Waters in Burlington, Ontario, and the National Hydrology Research Institute in Saskatoon, Saskatchewan. The Freshwater Institute had numerous field stations throughout the north to perform research on fisheries and water quality problems caused by hydroelectric reservoirs, overexploitation, and other human activities. The Canada Centre for Inland Waters began thorough investigations of the St. Lawrence – Great Lakes. The ELA was formed, becoming one of the few sites in the world where whole-ecosystem experiments could be done to investigate and solve pollutant and fisheries problems. This foresight caused great excitement in the global water science community: Canadian federal freshwater programs were envied throughout the world. Later, the Saqvaqjuac Program on the western shore of Hudson Bay began whole-lake experiments devoted to arctic freshwater problems.

Many Canadian university and provincial programs also became strong. The Ontario Ministry of Environment's Dorset Field Station alone had a staff of research scientists that compared with the most eminent laboratories in the world. The International Biological Program Char Lake Program, headed by the late Frank Rigler, was the first to investigate high-latitude lakes with the same thoroughness as the best temperate-zone programs.

Best of all, there was excellent interaction between federal, provincial, and university scientists, who worked together with contagious enthusiasm to develop the most powerful freshwater research teams anywhere in the world. This enthusiasm also developed excitement south of the border. Scientists from the Lamont–Doherty Earth Observatory, headed by Dr. W.S. Broecker, worked at the ELA for many years, providing a synthetic view of freshwater and marine and physical, chemical, and biological problems. Scientists from the universities of Kansas, Arizona, and Minnesota

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also had long-term programs at ELA. As a result of this spirit and competence, Canadian research and Canadian-trained scientists helped to solve water and fisheries problems in many areas of the world.

Unfortunately, these programs have been slowly strangled by a shortage of funds, poor salaries, and lack of replacement of departing staff. Politicians have stated the need to balance federal and provincial budgets as an excuse to reduce spending for environmental research and to decrease the size of the civil service.

Who is minding the store?

As any Canadian knows, a tiresome, juvenile turf war consumes much of the time of both federal and provincial politicians. Most of us do not care what level of government protects our resources, as long as there are not expensive overlaps, and no critical gaps are left. In aquatic science, gaps are a concern as we enter the new millennium.

Both federal and many provincial governments have simultaneously cut research budgets for freshwater research very severely in the 1990s. Environmental departments have been particularly hard hit because the effects are not as visible as in health care or education. As a result, there are huge gaps in research, monitoring, and synthesis of scientific information. In Ontario, federal laboratories have had reductions in funding and staff, especially for freshwater topics like acid rain, climate warming, and invading non-native species. Department of Fisheries and Oceans groups like the Bayfield Institute and the Experimental Lakes Project were particularly targeted, as the department transferred almost all of its resources to dwindling cod and salmon stocks. Their justification is that freshwaters are provincial responsibilities. But at the same time, the Ontario Ministry of Environment's Dorset laboratory, which has done some of the world's best research and monitoring on acid rain and eutrophication, has had severe budget cuts and staff layoffs.

In the prairies and in the West, the situation is little better. Winnipeg's Freshwater Institute has closed all of its field stations except for ELA. The National Hydrology Research Institute and other Environment Canada installations have totally inadequate budgets. Parks Canada has poor capability to assess or protect aquatic resources in our national parks.

Again, provinces have made simultaneous cuts. In Alberta, many critical monitoring functions have been handed off to industries to monitor their own effluents. Research budgets are very low. Many activities that were formerly done by Department of Environment staff are now contracted to consultants or left to industry to police itself.

Politicians have hidden the critical nature of these cuts behind the standard caricature of lazy, overpaid, and underworked civil servants, causing the public to shout "hooray," without questioning what might be lost. I personally find the lazy civil servant image to be infuriating, for many government scientists are among the hardest working individuals in society. They view first-hand the rate at which Canadian natural resources are being squandered, which has focused them on their tasks in a way that can only be compared with wartime activities in other sectors of society. Many of my colleagues worked many long hours each week without additional pay because they believed that what we were doing was important.

Some have expected university scientists to fill the void left by the erosion of government science. But Canadian universities have a primary mandate to teach, with research only a secondary activity. Faculty members are recruited to teach required courses, not to fill niches in large research teams. Most university research is designed to educate graduate students, who are only present for a few years. They must demonstrate creative ability, not continue monitoring programs. University scientists are forced to obtain more and more of their research funds from industry. Even the Natural Sciences and Engineering Research Council of Canada now puts much of its money into cooperative research programs, where matching funds by industry are an important criterion. These programs are probably fine for applied sciences and engineering, where the production of useful and marketable commodities is an objective. But these programs are uncomfortable fits with most environmental science in the public interest. Looking back, I wonder how many detergent companies would have co-sponsored research on eutrophication that required them to totally change their products? How many coal companies would have co-sponsored research to show that they were causing an acid rain problem? The question must be asked: what agencies today do science to protect the public interest? Answers for different regions range from fewer than there used to be to near zero. This situation must be reversed if we are to have sustainable water resources in the next century.

Research on northern great lakes: a national disgrace

Many Canadian waters are currently jeopardized by human intrusion, without proper documentation of their baseline state and how humans have altered their communities and biogeochemical cycles. There are many examples, but the northern great lakes are most conspicuous. Great Slave Lake, Great Bear Lake, and other large northern lakes are among the most unstudied freshwaters of the world. Canada spends more money on great lakes research in Africa and the former U.S.S.R. than it does on its own northern great lakes. Great Slave and Great Bear lakes are the only remaining great lakes in the world where non-native aquatic species have not invaded.

Great Slave Lake was last studied in detail by Rawson (1950, 1956). With small boats and primitive hand-operated equipment, Rawson and his students discovered most of what we know about the lake, which is not very much by modern standards. The lake is now threatened by nutrients from burgeoning communities, industrial effluents from the Peace–Athabasca River system, pollution from gold and diamond mines, and exploitation of fisheries.

Great Bear Lake has never been comprehensively studied. There is not even a vessel on the la' e that is capable of supporting research activity. The lake was polluted with uranium and radium from the Port Radium Mine in the early years of the last century. A few fishing lodges, the small indigenous community of Deline (formerly Fort Franklin), the abandoned mine facilities, and the ubiquitous inputs of airborne toxins are the only anthropogenic traces on the lake. At present, there are no roads or railways, but this will

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change rapidly. Clearly, it is the world's most pristine great lake at present. It is tragic that we know nothing about its aquatic communities and biogeochemical cycles, for if the twentieth century pattern of human activity continues, they will clearly be stressed in the present century. It is time that a major research institute focused on northern freshwaters and their problems.

How can a small country like Canada solve these problems?

It is well known that Canada's funds for research are a much smaller proportion of its national budget than in most First World countries. This must change for environmental science if we are to adequately protect Canadian resources from degradation (Peters et al. 1996).

Canadian universities, which are largely funded by provincial governments that see university education and research as being of peripheral value, will never be able to directly match the facilities of large American universities with enormous endowments or large environmental research facilities like Woods Hole or Scripps Institution. However, the combination of large federal and provincial environmental laboratories and universities offers some uniquely Canadian possibilities. Many government laboratories are on or near university campuses. Although individual government scientists often hold adjunct professorships and cooperate with university professors in research, such links have never been formalized. Universities have supplied much valuable research to ecosystem approaches at ELA and the Dorset field stations. In return, comprehensive government programs offer unique possibilities for interdisciplinary research and teaching, particularly at the graduate level. Some steps have been taken to explore these possibilities, for example, the linkages between Trent University and the Dorset Field Station of the Ontario Ministry of Environment and Laurentian University's Co-op Unit. But much more could be done.

Firstly, selection committees for new university scientists might be composed of both government scientists and university professors. With government scientists sharing some of the teaching load, scientists could be recruited with more emphasis on research specialty than is currently the case. The potential and inclination for interdisciplinary research and teaching could be among the selection criteria. Secondly, Natural Sciences and Engineering Research Council of Canada strategic grants and industrial grants or their equivalent might allow funding or in-kind support from government agencies to be used to "match" funds in its industrial and strategic grants programs, which currently only allow funding from industries to be counted. These would allow funds for research in the public interest, rather than only to support corporate agendas. Not only freshwater, but forestry, national parks, and other environmental programs could also benefit from such relationships.

I am optimistic that such arrangements might inject new life into aquatic and other environmental science in Canada. My experience with acid rain, eutrophication, and arctic research is that Canadian scientists generally do much more per dollar than their counterparts in other countries. Shoestring budgets are a tradition of environmental research in this country. But as we enter the twenty-first century, the shoestring is looking very worn. New programs in environmental science, particularly aquatics, are urgently needed if the destruction of Canadian freshwater ecosystems is to be prevented. Research must be much more focused on the cumulative effects of human activity than it has been in the past.

A national water strategy

Solving the water problem will require more than research. A national water strategy must be developed to get all levels of government to work cooperatively. Aboriginal people have been concerned about water issues for some time, for example, in the areas of Manitoba and Quebec flooded by large hydroelectric reservoirs and in the Peace–Athabasca drainage affected by pulp mills and oil sands developments. Corporations and the general public must become engaged. Until the Walkerton tragedy, the press paid little attention to water issues. The time to act is now, while there is widespread interest. Disappointingly, neither water nor other environmental issues have so far emerged in the political debates that have begun in anticipation of the election of a new national government. Unless there is a quick reversal of recent trends in water management, freshwaters will become Canada's foremost ecological crisis early in this century. I issue a challenge to future generations of aquatic scientists: the best thing that could happen to freshwaters in Canada is that you take steps to show that my predictions are wrong.

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Otoliths, increments, and elements: keys to a comprehensive understanding of fish populations?[1]

Steven E. Campana and Simon R. Thorrold

Abstract: The chronological properties of otoliths are unparalleled in the animal world, allowing accurate estimates of age and growth at both the daily and the yearly scale. Based on the successes of calcified structures as environmental proxies in other taxa, it was logical that researchers should attempt to link otolith biochronologies with otolith chemistry. With the benefit of hindsight, this anticipation may have been naive. For instance, the concentrations of many elements are lower in the otolith than in corals, bivalves, seal teeth, or the other bony structures of fish, making them less than ideal for elemental analyses. Nevertheless, there is growing interest in the use of otolith chemistry as a natural tag of fish stocks. Such applications are directed at questions concerning fish populations rather than using the fish as a passive recorder of the ambient environment and do not rely upon any explicit relationship between environmental variables and otolith chemistry. The questions that can be addressed with otolith chemistry are not necessarily answerable with genetic studies, suggesting that genetic and otolith studies complement rather than compete with each other. Thus, we believe that otolith applications have the potential to revolutionize our understanding of the integrity of fish populations and the management of fish stocks.

Résumé : Les propriétés des otolithes sur le plan de la chronologie sont sans équivalent dans le monde animal, car elles permettent d'estimer avec précision l'âge et la croissance à une échelle tant quotidienne qu'annuelle. Étant donné les succès obtenus par l'emploi des structures calcifiées comme substituts des conditions environnementales chez d'autres taxons, il était logique pour les chercheurs de tenter de faire le lien entre la biochronologie et la chimie des otolithes. Rétrospectivement, cette approche peut sembler naïve. Par exemple, les concentrations de nombreux éléments sont plus faibles dans les otolithes que dans les coraux, les bivalves, les dents de phoques ou les autres structures osseuses des poissons, ce qui en fait de bien mauvais candidats à l'analyse élémentaire. Toutefois, on note un intérêt croissant pour l'emploi de la chimie des otolithes comme marque naturelle des stocks de poissons. De telles applications visent à répondre à des questions sur les populations de poissons plutôt qu'à utiliser les poissons comme enregistreurs passifs du milieu ambiant, et ne se fondent pas sur une relation explicite entre les variables environnementales et la chimie des otolithes. Les questions auxquelles peut répondre la chimie des otolithes ne sont pas nécessairement abordables par l'étude génétique, de sorte que les travaux sur les otolithes et les études génétiques vont se compléter plutôt que se concurrencer. Nous pensons ainsi que les applications de l'étude des otolithes peuvent révolutionner aussi bien notre compréhension de l'intégrité des populations de poissons que la gestion des stocks halieutiques.

[Traduit par la Rédaction]

Introduction

The collection of age-structured information has always been a major preoccupation of fisheries science. Perhaps as a result, studies of fish have dominated progress in the field of age determination for several decades. To give some idea of the magnitude of the resources allocated to this activity, it is interesting to speculate on the global extent of age determinations based on otoliths. After an informal survey of 30 fisheries laboratories around the world, we have determined that a minimum of 800 000 otoliths were aged worldwide in 1999, at an approximate cost of $8 million CAN. An unknown but much larger number of scales and vertebrae were also aged, albeit at a considerably lower unit cost. On the basis of known numbers, well over 1 million fish were aged last year, and the actual number is probably closer to 2 million. In contrast, the number of individuals of other taxonomic groups that are aged on a routine basis, either as part of harvest calculations or otherwise, appears to be at least one to two orders of magnitude smaller. For example, only a few tens of thousands of nonfish aquatic animals (primarily bivalves) are aged annually in support of research or resource management. Age determinations of terrestrial animals are much lower in number again.

There are several reasons for the apparent emphasis on age determinations in the study of fishes compared with other animals. (*i*) Most fishes have life spans that exceed 1 year, and many have life spans of more than 20 years. As such, age and age composition are important characteristics of individuals and populations, respectively. The impact of the "baby boom" on human populations provides a useful analogy. (*ii*) Fish are much easier to age than most other organisms. For example, some animals such as the lobster lack

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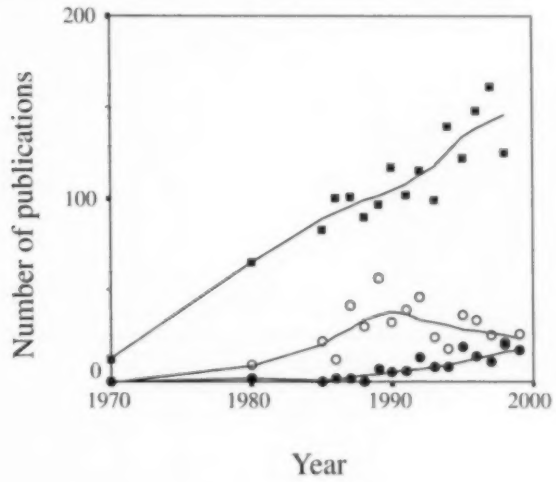
Fig. 1. Trends in annual numbers of primary publications describing otolith annuli (■), otolith microstructure (○), and otolith chemistry (●). On a percentage basis, otolith microstructure papers reached a peak in the late 1980s, while papers on otolith chemistry have been increasing steadily over the past decade. LOWESS curves have been fitted to each time series.



permanent or bony structures upon which age determinations can be based. (*iii*) Age, growth rate, and mortality rate (growth and mortality are both based on age information) are three of the most influential life history characteristics controlling the productivity of fish populations. Unlike birds and mammals, fish have indeterminate growth patterns that are heavily influenced by the environment. As a result, fish growth and production are less predictable than those of homeotherms and require frequent measurement if productivity calculations or population characteristics are to be adjusted for environmental change. For example, the impact of global warming on a hypothetical fish population might be to increase growth rate, reduce longevity, reduce the age of sexual maturity, and increase the rate of natural mortality. Without accurate age data, the net effect on the abundance and productivity of the population would be difficult to predict.

One might normally expect the progression of otolith research in the primary literature to be associated with the development and refinement of techniques for determining annual age, since otoliths provide the most accurate age determinations over the broadest age range (Secor et al. 1995). In fact, three separate otolith disciplines appear to have evolved over the past 100 years (Fig. 1). Beginning with Reibisch's observations of otolith annuli in 1899, there has been continued and growing interest in the use of the otolith as an indicator of annual age. Many applications in age estimation are now considered routine, even if accuracy continues to be an issue (Secor et al. 1995). With the development of otolith microstructure examination in the early 1970s, the otolith literature became preoccupied with this new approach and its capabilities for determining the daily age of a fish with unprecedented precision (Pannella 1971; Campana and Neilson 1985). In light of the similar focus on age-structured information in both of these disciplines, the evolution of microstructural work from macrostructural examinations appears logical. However, the relatively sudden development of otolith elemental analyses in the 1980s appeared not to follow such a logical progression. Relatively few of the elemental analyses to date have taken advantage of the otolith growth pattern, and at first glance, there is no obvious transition between the earlier otolith work and the elemental papers, which have increased exponentially in number during the past decade. How, then, to interpret this sequence of events?

The appearance of otolith chemistry as a significant theme in recent otolith research is probably not a simple consequence of the overall increase in number of age or otolith studies. Instead, we suggest that it has developed in anticipation of the otolith's properties as an environmental recorder, based almost exclusively on the successes of calcified structures as environmental proxies in other aquatic organisms (Chivas et al. 1985; Holmden et al. 1997; Dettman et al. 1999). We now know that there are few parallels between otolith chemistry and that of calcified material in aquatic invertebrates, at least beyond the superficial observation that both are composed primarily of calcium carbonate (Campana 1999). Nevertheless, elemental and isotopic assays of otoliths continue to increase in popularity, despite analytical requirements and a range of applications that appear considerably more restrictive than are present in similar studies of other organisms. So why is the pace of research in this discipline proceeding so quickly? As we will argue below, accelerated research into otolith chemistry applications is proceeding because of the unique chemical and chronological properties of the otolith. These properties, in turn, allow applications and questions to be answered that are simply not possible in other organisms or calcified structures. In the following pages, we offer an interdisciplinary overview of otoliths and otolith applications, which frequently strays across taxonomic and methodological boundaries. The intention is to provide a broad, and occasionally philosophical, perspective on the direction that the field has taken, as well as some thoughts on its future direction. A comprehensive review of the field is not the subject of this paper; that has been addressed elsewhere (Campana 1999). Rather, the goal is to contrast progress in the otolith field with that on other structures and other organisms and thus attempt to fathom why we have moved in the direction that we have.

General properties of calcified structures in aquatic organisms

Growth bands in calcified structures corresponding to daily, seasonal, or annual patterns are common in a number of aquatic phyla. Annual density or optical bands are found in coral skeletons, bivalve shells, and mammal teeth, as well as fish otoliths (Fig. 2). Otoliths are a focus of attention by fisheries scientists because of the precision of age estimates based on annuli and the relative ease of otolith preparation and annuli enumeration. Indeed, the clarity of annual increments in the otoliths of fish species from both marine (e.g., *Pogonias cromis*; Campana and Jones 1998) and freshwater habitats (*Aplodinotus grunniens*; Pereira et al. 1995) can be quite remarkable. Age estimates of 100 years or more have been recorded from several deepwater fishes based on otolith

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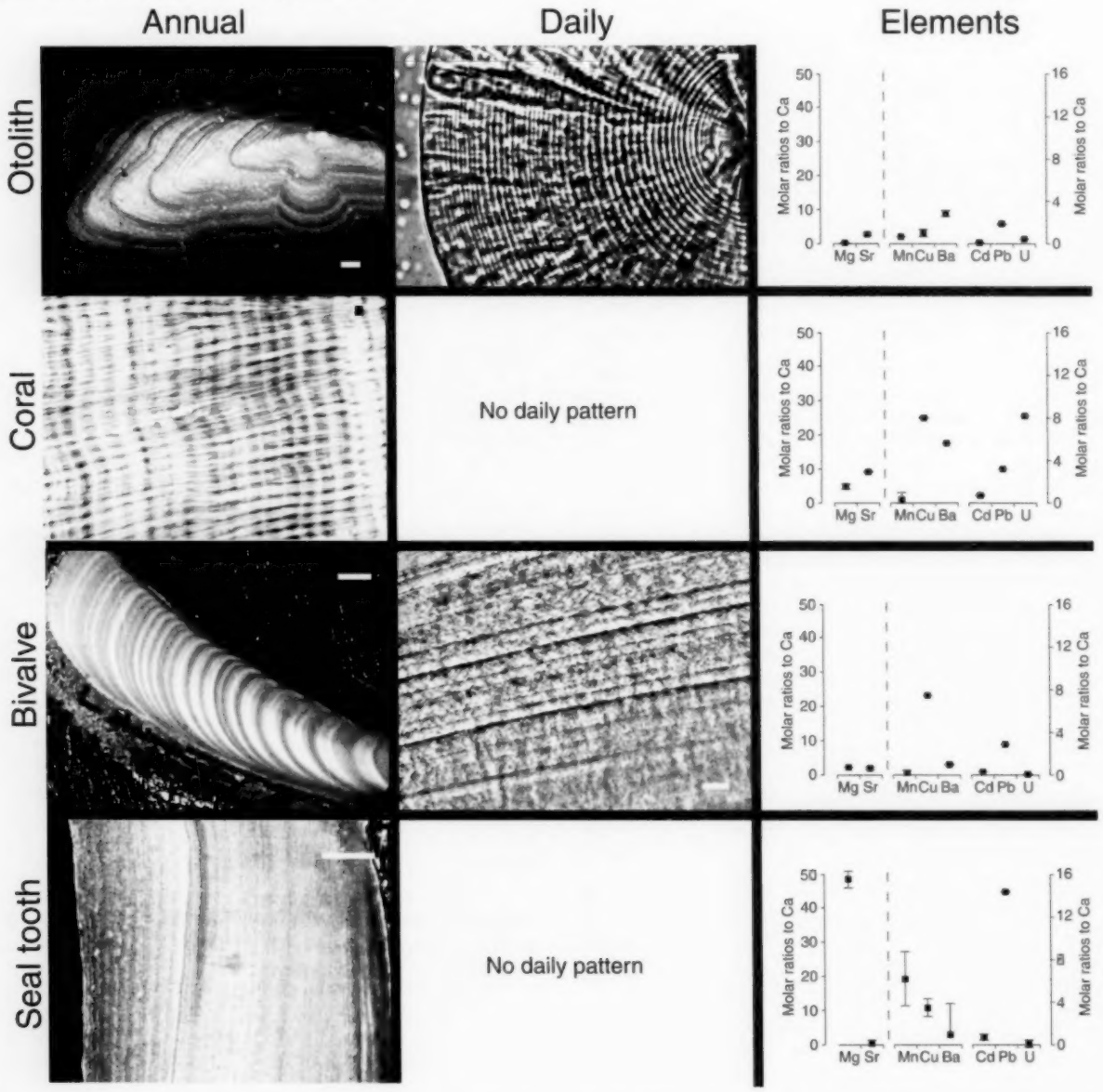
Fig. 2. Representative growth patterns and elemental composition of fish otoliths, corals, bivalves, and seal teeth at various scales. The images of annual patterns are from Atlantic cod (*Gadus morhua*), coral (*Siderastrea* sp.), Arctic surfclam (*Mactromeris polynyma*), and grey seal (*Halichoerus grypus*). The daily increment images are from Atlantic herring (*Clupea harengus*) and Arctic surfclam. Annuli are visible in all of the taxa, but consistent daily growth patterns were evident only in otoliths and bivalves. Scale bar = 1 mm for annual patterns and 10 µm for daily patterns. All elemental data are means of three replicate analyses of the same specimen (±SE), expressed as molar ratios to Ca (Mg:Ca, Sr:Ca ($\times 10^{-3}$); Mn:Ca, Cu:Ca, Ba:Ca ($\times 10^{-6}$); Cd:Ca, Pb:Ca, U:Ca ($\times 10^{-8}$)). Broken lines separate data referenced to left- and right-side *y*-axes.



annuli, while even tropical species routinely attain ages of 30 years or more. Although the accuracy of extremely old age estimates has been questioned, sensitive assays of bomb radiocarbon and ^{210}Pb:^{226}Ra ratios have generally confirmed longevity estimates where validation has been attempted (Campana 1999). Otolith annuli are narrow compared with annual bands in calcified structures of other organisms, often on the order of 20–50 µm in width (Fig. 2). This is indicative of a low rate of calcification, while the failure of otolith growth models based only on inorganic molecules and pH (Romanek and Gauldie 1996) suggests that otolith crystallization is under the control of soluble organic molecules within the endolymphatic fluid (Belcher et al. 1996; Falini et al. 1996).

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Daily growth increments in calcified structures are not as common as annual patterns and are restricted to species in which the depositional environment of the structure can be controlled by the organism without subsequent resorption (Fig. 2). Examples of such structures include fish otoliths (Campana and Neilson 1985), bivalve shells (Richardson 1988), and squid statoliths (Jackson 1990). Under normal circumstances, higher vertebrates do not produce daily growth patterns (Neville 1967). The presence of easily discernable daily increments in otoliths provides a remarkably accurate and precise method for age estimation of most larval and juvenile fishes (Campana and Neilson 1985). These data have been used to determine growth rates during early life history, estimate pelagic larval durations of reef-associated species, and examine the effects of physical processes on larval survival through back-calculation of hatch date distributions. It is also possible to reconstruct instantaneous daily growth rates of larval fish from increment width trajectories, based on an empirical relationship between otolith size and fish size (Campana and Jones 1992). Such information remains the envy of ecologists working on marine invertebrates where, for instance, information on larval durations is based on the time for pelagic larvae to reach competency when reared in the laboratory.

The chronological properties of otoliths are, then, unparalleled in the animal world. Therefore, it was perhaps only natural that researchers attempted to link this information with data on the environment inferred from chemical analyses of otolith growth increments. However, it is not immediately obvious that otolith geochemistry is influenced by processes similar to those affecting other calcified structures in either aquatic vertebrates or invertebrate phyla. We conducted a comparative, but cursory, analysis of the minor and trace element chemistry of a typical otolith, coral skeleton, bivalve shell, and seal tooth using laser ablation inductively coupled plasma mass spectrometry (ICP-MS). There were significant differences in the concentrations of divalent metal ions capable of substituting for Ca among each of the structures that we examined (Fig. 2). The scale of these differences was not sensitive to the particular species selected for analysis. The coral skeleton contained high levels of Sr and U, while Mg and Pb values were elevated in the seal tooth. Otoliths, however, were characterized by consistently low levels of all these ions, confirming Campana et al.'s (1997) observation that otolith aragonite is relatively free of trace metal contaminants. This observation does not imply that otolith chemistry fails to record temperature or water composition, since correlations between otolith and water chemistry may still exist even if absolute levels of elements are different. Nonetheless, the data highlight the fact that otolith elemental analyses remain challenging compared with assays of other calcified structures. Many of the elements of interest, including those likely to be indicative of pollution exposure such as Ni, Cu, and Pb, are present in concentrations at or below the detection limits of even the most sensitive mass spectrometers (e.g., Sie and Thresher 1992; Thorrold and Shuttleworth 2000).

Given the analytical constraints associated with otolith chemistry, might other calcified structures provide more information on environmental conditions experienced by individual fish? Preliminary studies on the chemistry of vertebrae (Mulligan et al. 1983) and scales (Wells et al. 2000) suggest that both structures have promise. To provide a baseline comparison of the chemical composition of each of these structures, we analyzed scales, vertebrae, and otoliths from juvenile spot (*Leiostomus xanthurus*) reared under controlled laboratory conditions using solution-based ICP-MS (Fig. 3). Here, as would be expected of any fish species, otoliths were characterized by lower levels of Mg:Ca, Mn:Ca, and Ba:Ca than either scales or bones. Again, however, it was also clear that otoliths provided superior chronological records, either at the daily or at the annual level (or both) (Fig. 3).

Unique properties of the otolith

There is little doubt that current interest in otolith chemistry is driven by the chronological capabilities of these structures rather than any unique chemical properties. Nonetheless, otoliths do have several properties that set them apart from all other skeletal structures and without which many of the current applications would be impossible.

Otolith growth is continual

In part, this is because the otolith is one of the few calcified structures that is nonskeletal. The shells of bivalves, the tests of coral, and the bones of fish and mammals all serve key support or protection functions for their host. Since the growth of skeletal elements necessarily conforms to that of the organism, there is no requirement for continued growth during periods of nonfeeding or poor growth. The same principle applies to scales and teeth. In contrast, it appears that otolith growth is maintained even through periods when somatic growth is nonexistent (Maillet and Checkley 1990), and if not daily in old fishes, then at least seasonally. The advantage of a continuous growth pattern is most evident in studies of old fish in which annulus counts from scales and bones grossly underestimate those visible in the otolith (Beamish and McFarlane 1995). Clearly, a complete chronology is required if the environment corresponding to a previously deposited growth increment is to be accurately dated.

Could the unique and continued growth of the otolith be due to its nature as an organ of balance? Perhaps. For reasons that are still unclear, the vestibular organs of the fish (three otolith pairs) and squid (statolith pair) are the only calcified structures known to grow throughout the lifetime of the animal. Presumably, this is a reflection of their unique mode of calcification — a form of biomineralization with no epithelial contact, which is rarely encountered in other taxa or structures (Payan et al. 1997; Campana 1999). The fact that otolith growth is tightly linked to the natural endocrine rhythm of the fish (Campana and Neilson 1985) is probably also relevant, although the cause–effect relationship is unclear.

Otolith growth occurs in isolation from the environment

This property of the otolith is clearly not shared by calcified exoskeletons, scales, or teeth, but perhaps surprisingly, nor is it shared by bones. While the bones of a fish or mammal are not in direct contact with the external environment, they are exposed to the physiological environment of the organism much more than in the case of the otolith. Only the

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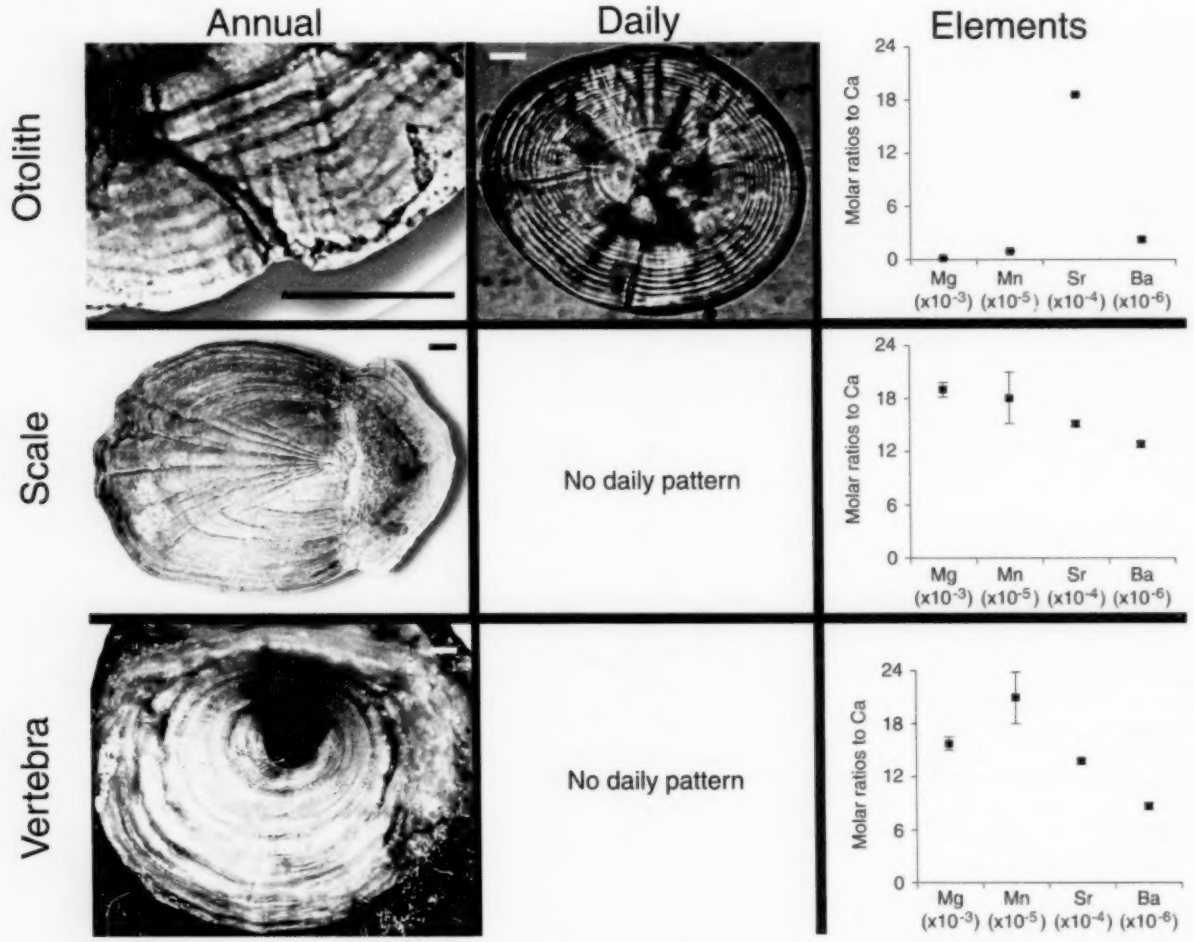
Fig. 3. Representative annular growth patterns of otoliths, scales, and vertebrae from a tautog (*Tautoga onitis*). The otolith daily growth pattern is from a larval haddock (*Melanogrammus aeglefinus*), while the elemental assays (mean ± SE) are based on otoliths, scales, and vertebrae from each of three young spot (*Leiostomus xanthurus*) reared in the laboratory. Scale bar = 0.5 mm for annual patterns and 10 µm for daily patterns.



otolith is isolated within a semipermeable inner ear membrane and bathed in an endolymphatic fluid that is considerably more regulated than is the composition of blood plasma (Payan et al. 1997; Campana 1999). Presumably, the physical and chemical isolation of the inner ear is a prerequisite of its unique mode of calcification. However, it seems likely that such a level of isolation from the environment is not ideally suited for tracking environmental conditions.

The otolith is not subject to resorption

Lack of resorption is a prerequisite for the preservation of a complete growth and environmental record. This is probably the most important property of the otolith and is one that is not shared with any other calcified structure in fish or other vertebrates. Even periods of starvation, which can result in resorption of scales and bones (Bilton 1974), do not resorb previously deposited otolith material (Campana and Neilson 1985). Of course, the acellular nature of the otolith sets it apart from bone and teeth, which are always susceptible to metabolic reworking. Biomineralization in most invertebrates is also acellular, thus ensuring that resorption due to metabolic causes does not occur.

The crystalline structure of the otolith is aragonite

Of the three crystalline forms of calcium carbonate found in otoliths and other calcified structures, it is the metastable aragonite form that makes up all of the otoliths used in age and environmental studies (Carlström 1963). Aragonite is also found in coral and sclerosponge skeletons, bivalve shells, and squid statoliths. However, among the vertebrates, only the aragonitic otoliths of teleosts are useful age indicators; fish more primitive than teleosts have calcitic otoconia, while more advanced vertebrates have otoconia composed of hydroxyapatite. This apparent quirk of evolution is not necessarily an advantage, although the slightly higher specific gravity of aragonite (2.93) over that of calcite (2.71) and

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vaterite (2.65) may be related to the otolith's role as a gravity receptor. There is no obvious reason why aragonitic otoliths would serve as superior recorders of age or environmental conditions compared with any other polymorph of calcium carbonate. Yet there is no question that the mode of calcification in aragonitic otoliths is unique compared with other biomineralized structures (Suga and Nakahara 1991). Similarly, the intricate and highly species-specific shape of aragonitic otoliths is both striking and puzzling (Harkonen 1986). While the diverse shapes are obvious indicators of a carefully controlled biomineralization process, there is no known function for the diversity in size and shape across species. Nevertheless, it is tempting to speculate that the combination of species-specific shapes, aragonitic composition, and unique method of calcification is indirectly responsible for the time-keeping and environmental recording properties of otoliths.

Otolith chronologies and environmental reconstruction

Otoliths provide some of the best examples of biochronologies in the animal kingdom, combining annual sequences of up to 110 years in adult fishes (Boehlert et al. 1989; Pereira et al. 1995) with daily chronologies of up to a year during the larval and juvenile stages (Campana and Neilson 1985). It was perhaps only natural that researchers should attempt to link this information with data on the temperature or water composition inferred from chemical analysis of otoliths sectioned to reveal the growth increments. These endeavors were initially predicated, often explicitly, on correlations between temperature or water chemistry and the elemental composition of biogenic aragonite found in the skeletal material of marine invertebrates such as corals (Radtke 1989). However, as we have demonstrated, the chemistry of otolith aragonite is quite different from the aragonite found in the skeletal material of marine invertebrates. Are there reasons, then, to believe that otolith chemistry is a function of the environmental conditions experienced by individual fish? The answer would appear to be a strongly qualified "yes."

Despite statements to the contrary (Thresher 1999), it is indeed possible to reconstruct environmental histories from otolith chronologies. For instance, stable isotopes of oxygen in otoliths are deposited close to isotopic equilibrium and with a well-defined fractionation effect due to ambient temperature (Patterson et al. 1993; Thorrold et al. 1997*a*). Several studies have used stable isotope analyses of oxygen isotopes to reconstruct temperature histories in both ancient and modern water masses (Patterson 1998; Weidman and Millner 2000). Experimental evidence indicates that otolith chemistry is also an accurate proxy for concentrations of at least some trace elements (e.g., Sr, Ba) in the ambient environment (Farrell and Campana 1996; Bath et al. 2000). Otolith Sr, for example, serves as an excellent proxy for ambient salinity and has often been used to reconstruct a history of anadromous migrations (Secor 1992).

There is also good reason to believe that interpreting geochemical records from otoliths will be more difficult than from other environmental proxies such as invertebrate skeletons. Indeed, given the number of opportunities for significant decoupling, it is perhaps surprising that any detectable relationship exists between water and otolith chemistry. For instance, otolith aragonite precipitates from the endolymphatic fluid, the composition of which is regulated by membranes that separate the blood plasma from the ambient environment and the endolymphatic fluid from the blood plasma. It is possible, however, that Ca analogs such as Sr and Ba are moving across these membranes via para- or trans-cellular Ca channels (Kalish 1991; Mugiya and Yoshida 1995), in which case the environment may be able to exert a strong influence on subsequent element:Ca ratios in the otolith. There is also the likelihood of physiological processes altering levels of organic ligands, and hence free ion concentrations, within the blood plasma (Kalish 1991). In a serendipitous finding, at least for otolith researchers, it appears that the endolymphatic fluid is buffered from at least some of the temporal variability that characterizes the chemistry of the blood plasma (Payan et al. 1997). Aquatic environments are, in turn, less subject to high-frequency ("white noise") environmental variations than are the norm in terrestrial habitats, which may also increase the signal-to-noise ratio of chemical proxies in otoliths compared with the skeletal structures of terrestrial organisms.

Taken together, there appears to be hyperbole on both sides of the debate concerning the environmental effect on otolith chemistry. We believe that a consensus is emerging that while some elements in otoliths are useful as proxies of ambient environmental conditions, many, and perhaps most, elements are linked to the environment either indirectly or not at all (Campana 1999). So why are so many people carrying out elemental and isotopic analyses of the otolith? For at least two reasons: the excellent chronological properties of otoliths and the observation that otoliths appear to be immune to resorption. These two properties are unparalleled by any other skeletal structure in fishes and have provided fisheries ecologists the opportunity to address questions that were simply not possible with either scales or vertebrae. As such, the fact that otolith research evolved from studies of annuli to daily growth increments to elemental analyses was not a coincidence. Rather, it was a reflection of the importance of age-structured spatial information to studies of fish. Yet as we discuss below, there is a third reason for the growing interest in otolith composition, and it has to do more with the question being asked rather than the means for answering it.

What's the question: the fish or the environment?

Given that only a handful of elements are likely to be useful in reconstructing environmental history, is it possible that data on otolith chemistry could be useful even if it were not possible to make detailed inferences about the physicochemical environment? The recent explosion of papers using otolith chemistry suggests that this is the case. Certainly the questions being tackled with otolith geochemistry are very different from those being addressed with other environmental proxies. Chemical assays of invertebrate and mammal skeletons tend to be used to infer some feature of the environment, whereas chemical assays of otolith are directed at questions concerning the fish itself. For example, oxygen

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isotope assays of coral annuli are generally used to reconstruct the temperature regime of the local ocean (Leder et al. 1996), trace metal assays of bivalves serve as pollution sentinels (Brown and Luoma 1995), and radioisotope assays of mammalian antlers indicate the extent of nuclear fallout (Tiller and Poston 2000). In each case, the interest is in the location or environment, not the organism being assayed. In contrast, otolith assays have been directed at questions concerning fish migration patterns (Thorrold et al. 1997*b*) or the extent of mixing between populations (Edmonds et al. 1991), where the focus is squarely on the fish. Indeed, the potential for significant migration, in both vertical and horizontal directions, has meant that the few attempts to reconstruct the environmental conditions of a given location from otolith chronologies have been from freshwater environments, where fish movements are constrained (Patterson et al. 1993; Patterson 1998).

By now, it should be clear that assays of otolith geochemistry are being used to address questions about fish that are simply not suited to assays of other organisms. Nevertheless, it has also become clear that these applications are driving otolith research well beyond what one would normally expect based on the chemical properties of otoliths. Is this an example of expectations not matching reality, or of inappropriate methods being used to address difficult issues? Not at all. Instead, we argue that the questions being addressed would be difficult or impossible to answer through other means. To support this statement, we offer three examples.

Atlantic cod (*Gadus morhua*) stock mixing

In a recent study, the trace element composition of the otolith (the elemental fingerprint) was used to track and identify members of four adjacent Atlantic cod stocks during a winter mixing period, using the fingerprints of the spawning aggregations as a reference (Campana et al. 1999). In this study, the elemental fingerprint was used as a natural tag, with many of the same strengths and limitations of conventional tagging, but with the advantage of a very large sample size of recaptures ($n \approx 2700$). Concurrent microsatellite DNA studies of the same fish were less able to distinguish among the various populations (Ruzzante et al. 1999), presumably because of periodic mixing among the spawning aggregations.

Weakfish (*Cynoscion regalis*) natal homing

Isotopic and elemental fingerprints of juvenile weakfish otoliths collected in their natal estuary were used to characterize and differentiate among adjacent estuarine habitats along the east coast of the United States (Thorrold et al. 1998). Several years later, adult weakfish from the same year-classes were collected when they returned to spawn in the estuaries. Otolith cores corresponding to the juvenile phase of the adults were assayed and the resulting fingerprints compared with reference fingerprints from the year in which the adult fish were spawned. A high degree of homing to natal estuaries (>85%) was demonstrated in some, but not all, of the subpopulations. Concurrent analyses of hypervariable markers, including microsatellite DNA and introns, were unable to detect significant genetic heterogeneity among juveniles from the various estuaries. These results were entirely consistent with a metapopulation model of weakfish population structure in which genetic exchange was accomplished through less than perfect natal homing.

Recruitment of coral reef fish

To determine the extent of local recruitment by a damselfish (*Pomacentrus moluccensis*) with a pelagic larval phase, Jones et al. (1999) chemically marked the otoliths of millions of developing embryos spawned around Lizard Island on the Great Barrier Reef. The ratio of marked to unmarked otoliths in fish collected immediately before settlement on the same reef tract was then used to estimate the relative contribution of recruits from the local area. This study was not only the first to demonstrate that larvae do actually return to their natal reef, but also suggested that the rate of self-recruitment of *P. moluccensis* to Lizard Island may be as high as 60%. No other study to date has been able to properly address this issue.

In these three examples, the successful results of each study took advantage of the chemical and (or) time-keeping characteristics of the otolith. In both the Atlantic cod and weakfish examples, otoliths were used as natural tags. These studies required only that the elemental and isotopic fingerprints from the reference samples were sufficiently different to allow unknown fish to be accurately classified to either a stock or a natal estuary. Although variations in the physicochemical environment probably generated the distinctive fingerprints, it was not necessary to reconstruct any aspect of the environment based on the otolith chemistry assays. It is conceivable that conventional tagging could have been carried out to produce similar results, but at a prohibitive cost. Why were the genetic approaches unsuccessful? Genetic markers are, of course, the archetypal natural tags and have been used to remarkable advantage in many population-level studies. Yet the failure of the genetic approach in each of the above studies was not at all surprising. As noted in the review by Ferguson and Danzmann (1998), genetic markers are ideally suited for many questions, particularly those focused on parental or evolutionary linkages, but are not necessarily well suited to localized stock identification or mixing issues. In particular, genetic markers would not be expected to perform well in instances where there is significant mixing among the groups of interest (e.g., among stocks). That was certainly the case in the above examples, where mixing rates were shown to exceed 1%. So for these types of studies, genetic markers were neither capable of nor appropriate for the question being asked. Are we suggesting that otolith elemental fingerprints are somehow superior to genetic assays? Not at all. In the absence of differences among groups, neither genetic nor otolith assays can be interpreted in terms of the similarity/dissimilarity of the groups. However, if differences exist, genetic analyses can be used to infer population structure, whereas elemental differences cannot. By corollary, the genetic structure of a population would be expected to remain relatively stable from year to year, whereas the corresponding elemental fingerprint might change. Therefore, genetic differences can be used to characterize populations, while differences in the elemental fingerprint merely reflect a different environmental history, which may or may not apply to the entire population. On the other hand, otolith elemental fingerprints formed under environmental influence are well suited for tracking those same populations, or subsets thereof,

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whether or not genetic differences are evident. So for tracking and mixing applications, the unusual properties of the otolith must be viewed as an advantage.

In conclusion, otoliths have become an indispensable tool to fisheries scientists. Otolith biochronologies provide information on age and growth with unparalleled precision and accuracy. Although the analysis of age composition data based on otolith growth increments is routine in many laboratories around the world, it is easy to forget that the number and complexity of age-structured analyses of fish are matched only by age-structured studies on human demographics. The chemical composition of otoliths also affords the possibility of environmental reconstructions that, when matched with otolith biochronologies, may allow an individual fish to be retrospectively positioned in space and time throughout its life. We are clearly some way from realizing this goal. Nonetheless, the application of otolith chemistry as a natural tag is already providing unique information on spatial distributions at the population level. We believe that this information will not only increase our understanding of the integrity of fish stocks, but may also fundamentally alter the way that we view the assessment and management of exploited fish populations.

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Cultivation/depensation effects on juvenile survival and recruitment: implications for the theory of fishing[1]

Carl Walters and James F. Kitchell

Abstract: Large, dominant fish species that are the basis of many fisheries may be naturally so successful due partly to "cultivation effects," where adults crop down forage species that are potential competitors/predators of their own juveniles. Such effects imply a converse impact when adult abundance is severely reduced by fishing: increases in forage species may then cause lagged, apparently depensatory decreases in juvenile survival. Depensatory effects can then delay or prevent stock rebuilding. Cultivation effects are apparently common in freshwater communities and may also explain low recruitment success following severe declines of some major marine stocks such as Newfoundland Atlantic cod (*Gadus morhua*). Risk of depensatory effects should be a major target of recruitment research, and management policies should aim for considerably higher spawning abundances than has previously been assumed necessary based on recruitment data collected during adult stock declines associated with fishery development.

Résumé : Le succès des grosses espèces dominantes de poissons qui sont à la base de nombreuses pêches peut être dû en partie à un « effet cultural », les adultes récoltant les espèces fourrage qui sont des concurrents ou des prédateurs potentiels de leurs propres juvéniles. Cet effet a par contre un impact inverse lorsque l'abondance des adultes est fortement réduite par la pêche : les augmentations chez les espèces fourrage peuvent causer des baisses décalées dans le temps, à caractère apparemment dépensatoire, de la survie des juvéniles. Les effets dépensatoires peuvent alors retarder ou empêcher le rétablissement des stocks. L'effet cultural semble courant dans les communautés dulcicoles et peuvent aussi expliquer le faible succès de recrutement qui suit les déclins graves de certains grands stocks marins comme la morue franche (*Gadus morhua*) de Terre-Neuve. Le risque d'effets dépensatoires devrait être un thème majeur de la recherche sur le recrutement, et les politiques de gestion devraient fixer pour objectifs des abondances de géniteurs considérablement plus élevées que ce qu'on jugeait jusqu'ici nécessaire en se fondant sur les données de recrutement recueillies pendant les déclins de stocks d'adultes associés au développement des pêches.

[Traduit par la Rédaction]

Introduction

Single-species stock assessments and harvest policy development generally assume either that recruitment is independent of stock size or that recruitment varies around some compensatory relationship described by a simple saturating or dome-shaped curve. Compensatory effects are assumed to arise through reductions in intraspecific competition and (or) cannibalism when abundance is reduced by fishing. There is now broad empirical support for limits to compensatory response, so that low parental stock sizes can indeed result in lower mean recruitment (Myers and Barrowman 1996; Myers et al. 1999), so most assessments include a recruitment relationship that at least recognizes some risk of recruitment overfishing. But there has been little empirical support for the existence of "depensatory" or "recruitment failure" effects where recruitment decline with stock size is even more rapid than expected from a decrease in egg production combined with high juvenile survival (Myers et al. 1995*a*, 1995*b*; Liermann and Hilborn 1997). However, such effects are likely to be difficult to detect in typical data sets that have few observations at very low stock size (Shelton and Healey 1999). Depensatory effects are not routinely incorporated in assessments except via risk management tactics such as setting arbitrary minimum population size goals. The approach of assuming "stationary" mean stock–recruitment relationships has been criticized on grounds that it does not account for effects of either persistent environmental change or changes in trophic relationships (juvenile predation risk, food) that might accompany overfishing (e.g., see Walters 1987; Walters and Korman 1999; Hall 1999), but criticism has focussed mainly on our inability to forecast short-term recruitment changes. In particular, we have paid little attention to the risk of very severe nonstationarity, in the form of persistent depensatory effects (low juvenile survival) that develop with some time lag following periods of adult stock depletion.

Using Ecosim II (Walters et al. 1997, 2000), we have been conducting exploratory simulations to detect possible depensatory recruitment effects due to trophic interactions.

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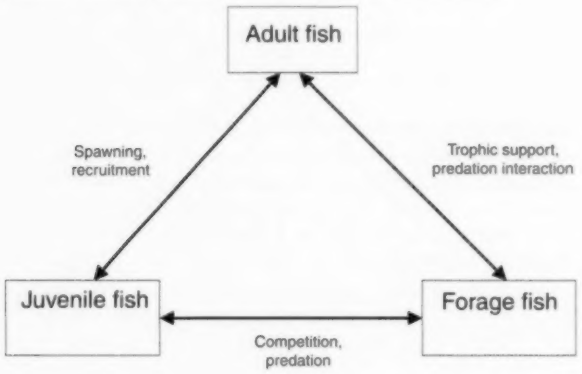
Fig. 1. We envision recruitment depensation at low stock sizes as arising from a trophic triangle: prey organisms of adult fishes can respond positively to reductions in adult fish abundance by fishing and then causing reductions in juvenile survival via competition and (or) predation interactions with the juveniles.



This model combines simple biomass dynamics models for some ecosystem components with age-structured (delay-difference) models for selected species that have strong trophic ontogeny and (or) size-selective fishing impacts. It links recruitment to trophic changes by explicit (and reciprocal, predator–prey) representation of how dynamic changes in food availability and predation risk affect juvenile mortality rates and how juvenile fish may moderate these rates through risk-sensitive changes in foraging times (Walters and Juanes 1993). Most often, the "emergent" stock–recruit relationships predicted by Ecosim II look like the classic Beverton–Holt, broken stick, or Ricker relationships, i.e., we predict mainly strong compensatory (stabilizing) effects due to the usual mechanisms thought to result in increased juvenile survival at low densities (more food, less cannibalism, etc.). But in some cases, we see a catastrophic pattern: as simulated fishing mortality rate is increased over time, recruitment initially appears to be stable or declining along a Beverton–Holt or Ricker relationship with declining spawning stock. But then, juvenile mortality rates "suddenly" increase (over a few simulated years) after some time delay to result in delayed depensatory effects that may result in extinction even if fishing is stopped.

Here, we describe the mechanism that causes models like Ecosim II to predict depensatory recruitment changes that strongly contradict classic compensatory stock–recruitment theory. We propose a "cultivation hypothesis" to suggest why this mechanism could in fact be quite common, especially for large, predatory fish species, and discuss factors that may prevent it from operating in some circumstances. We review case examples where it may have occurred. We conclude that the mechanism is plausible enough, and supported by enough circumstantial case evidence, to warrant immediate policy response in the form of higher spawning stock (lower exploitation rate) goals than would be estimated from single-species population theory.

How juvenile trophic interactions can cause depensatory dynamics

Delayed depensatory effects arise in Ecosim II models (Appendix) through the following sequence of events. As fishing reduces the adult population size of a fish species, the total number of juveniles produced per time decreases. In the absence other trophic effects, this results in increased food density in the localized "foraging arena" habitats (usually near predation refuges; see Walters and Juanes 1993) where juvenile feeding is concentrated. Juveniles respond to increased food density by reducing feeding time and hence time at risk to predation (or total time spent at body sizes small enough to be vulnerable to high predation risk). Juvenile mortality rate then decreases, so net recruitment at first stays nearly constant despite fewer juveniles entering the juvenile life stage per time. But if adult abundance is severely reduced, one or more smaller "forage fish" species are "released" to increase in abundance. Then, one or two negative effects can occur. First, the forage fish may directly (even if incidentally) prey on the juveniles, causing increased predation risk per time spent foraging and hence higher juvenile mortality rate. Second, if the forage and juvenile fish share at least some foods (e.g., zooplankton, benthic invertebrates) and use overlapping foraging arenas and tactics for reducing predation risk, increased forage fish abundance leads to reduced food density and hence to increased juvenile foraging time and general predation risk. A simple way to visualize this dynamic is as a "trophic triangle" (Ursin 1982; Cohen et al. 1993; He et al. 1993; Rudstam et al. 1994), "competitive juvenile bottleneck" (Bystroem et al. 1998), or "predator–prey role reversal" (Barkai and McQuaid 1988). The triangle adds prey/competitor dynamics to the usual juvenile/adult dynamic linkage that has traditionally been emphasized in population dynamics modeling (Fig. 1).

Figure 2 presents a graphical model for the elements of this mechanism, in terms of patterns that should be observable in the field if it is operating: (*i*) negative relationship between forage fish abundance and adult abundance ("spawning stock" biomass), (*ii*) depensatory increase in juvenile foraging time (and (or) reduced juvenile growth rate) as the forage fish become more abundant, and (*iii*) declining juvenile survival rate when adult abundance has been low for long enough for the forage fish increase to occur. Additionally, we should be able to observe (*iv*) diet and habitat use overlap between the juvenile fish and the forage fishes and (or) (*v*) direct evidence of predation by the forage fish on juveniles, in stomach contents sampling. Of these observations, we should not be surprised if direct evidence of predation is not found. Forage fish are likely to be much more abundant than the juveniles (and to have high food consumption rates) and may thus cause a high juvenile mortality rate (eat a large total number of juveniles) even if only a very tiny percentage of their diet is juveniles.

Note that this mechanism for causing decreased reproductive performance at low stock size is quite different from the common concern that fishing too hard on a dominant species may allow competitors to increase and "take over" its niche. We are talking not about competitors in general, but very specifically about other small fish (and some invertebrates like squid) that are likely to be directly impacted in abundance and distribution by adults of the fish species in question. These species may be direct competitors and (or) predators of the juveniles of the species during a life history stage where we know from recruitment experience that the

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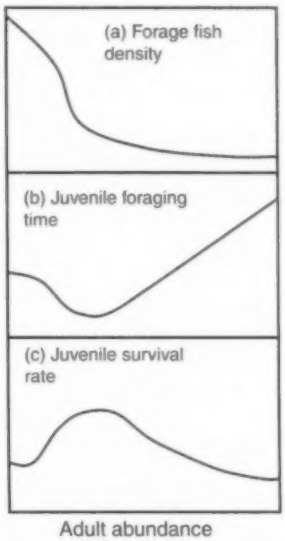
Fig. 2. Elements of a hypothesis for depensatory recruitment changes at low stock sizes. (*a*) Increase in abundance of small "forage" fishes/invertebrates if predatory stock size decreases; (*b*) increasing rather than decreasing juvenile foraging time when adult abundance is low due to competition with forage fishes; (*c*) decreased juvenile survival rate at low adult population size due to increased foraging time and (or) direct predation by forage species.



juveniles are likely to be "sensitive" (to have high and strongly density-dependent mortality rates). In part, this is not a new idea or concern: biologists have long speculated about how predatory fish species are able to achieve large body sizes, given that their juveniles must grow through a predation–competition "bottleneck" involving the very species that will be their prey later in life (Crowder et al. 1992; Wooten 1994). It is familiar in management procedures designed to create "balanced" predator–prey interactions such as those for bluegill (*Lepomis macrochirus*) – largemouth bass (*Micropterus salmoides*) systems (Gutreuter and Anderson 1985), as guidance for size at stocking procedures (Madenjian et al. 1992), and to ecologists engaged in evaluating "size-structured" or "trait-mediated" interactions (Persson and Eklov 1995; Werner 1998).

We can of course envision more complex mechanisms by which impacts of adult abundance on trophic structure may modify survival conditions for their juveniles. For example, we found in early Ecosim tests that invasion of Nile perch (*Lates niloticus*) in Lake Victoria was possibly slowed initially by competition/predation from the natural fish community of the lake. Population growth rate then apparently increased as the perch became abundant enough to depress this community and allow increases in an invertebrate (*Caridina*) and a fish (*Rastrinebola*) that later became its dominant foods (Kitchell et al. 1996; Walters et al. 1997). Another example would be the possibility of trophic "quadrangles" in zooplanktivores: if adults feed selectively on larger zooplankters, reduction in adult abundance may allow an increase in abundance of these larger forms with an attendant negative impact on abundance of smaller zooplankters that are needed by smaller juveniles. A third example is argued to account for the progressively increased juvenile mortality rates observed for stocked lake trout (*Salvelinus namaycush*) in Lake Superior. After sea lamprey (*Petromyzon marinus*) and fisheries mortality were reduced, natural reproduction allowed a gradual increase in adult abundance of a deepwater trout race (siscowet). This created a predator population that imposed increased mortality on the stocked juveniles of the shallow water trout race (lean) and may be responsible for the lack of successful reproduction by the latter (Hansen et al. 1995).

The depensatory mechanism described in Fig. 2 is fundamentally different from models for direct depensatory predation effects based on the form of predator responses to prey densities (Fig. 3) (e.g., Collie and Spencer 1993; Spencer and Collie 1997*a*, 1997*b*) or models based on reproductive failure at low population size. In classical "reaction vat" models of predator–prey interaction, decreasing prey mortality rate with increasing prey density is caused by increased handling time or satiation of predators, such that the proportion of the prey population killed by each predator decreases with increasing prey (juvenile fish) density (Fig. 4). This may occur in a few circumstances where prey are particularly vulnerable to predation and predators can be "overwhelmed", for example, during downstream migrations of salmon fry from small streams (Neave 1954), but it is probably not common. In Ecosim, we assume that predation takes place largely in spatial patches or "foraging arenas" where juveniles are forced to accept predation risk in order to forage and where predation rates are limited not by predator satiation but rather by juvenile movement rates into and out of (or time spent in) behavioral refuges and by predation risk per time spent foraging (see Appendix; also see fig. 1 in Walters and Juanes 1993). We think that this model for spatial organization is a much better description of general natural history experience in aquatic ecology (stomach contents data rarely show predator satiation, juvenile fish distributions obviously dominated by tactics to reduce predation risk) than is the classic reaction vat model. Further, it better explains the ecosystem-scale observation that trophic cascade effects are relatively weak and suggestive of ratio dependence in predator–prey interactions (McCarthy et al. 1995; Scheffer and De Boer 1995; Brett and Goldman 1996).

Why perverse interactions could be common: the cultivation hypothesis

Most fisheries develop at least initially to take the largest, most abundant, ecologically "dominant" fishes. This may be precisely the suite of species most vulnerable to depensatory responses because a reversal of these responses may be why such species are dominant in the first place. That is, ecological dominance may well be due at least partly to "cultivation effects": dominants may be species that are fortuitously capable of being especially good at capturing (and otherwise suppressing) the particular smaller forage fishes that could cause the worst competition/predation effects on their own juveniles. Note that this is not a group or population selection argument about selection favoring adults that consume particular forage species so as to protect their own juveniles.

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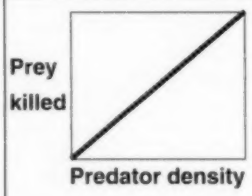
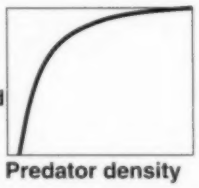
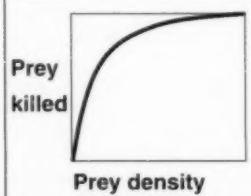
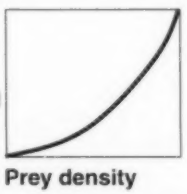
Fig. 3. Contrasting assumptions and predictions in models that explain depensatory effects by the form of predator functional responses in random search (reaction vat) environments versus models that assume spatial organization of predation interactions in patchy "foraging arenas."

Effect of:	Classical predator-prey "reaction vat" models	"Foraging arena" models
Predator density		
Prey density		
Implications	Depensatory increase in prey mortality rate at low prey densities; prey mortality rate highly sensitive to predator abundance; predator satiation common when prey abundance high	Compensatory decrease in prey mortality rate at low prey densities; prey mortality rate relatively insensitive to predator abundance; predators rarely satiated

It simply says that if there are several large species in a system, with varied diets as both juveniles and adults, the dominant large species should end up being that one that happens to cultivate the best survival conditions for its juveniles by having particularly large impacts on its juveniles' competitors/predators.

We usually think of dominant fishes as those capable of best using trophic (food) production and physical habitat and of being long-lived enough to accumulate large unfished population sizes. But when we make this assumption, we ignore the large body of evidence that abundance is generally "limited," not at the adult stage but rather at the juvenile stage (recruitment most often observed to be independent of or flat across a wide range of adult abundance). Dominance may well require adult feeding patterns that efficiently use production by lower trophic levels, but it certainly also requires relatively good conditions for juvenile survival and growth. The cultivation hypothesis is that dominance is a result of not only being able to acquire trophic resources but also to insure the best possible trophic conditions for juveniles.

Factors that mitigate against cultivation/depensation effects

An obvious and immediate objection to the cultivation/depensation arguments presented above is that they offer no mechanism by which large, dominant species could become abundant enough to have cultivation effects in the first place. Why is the world not dominated by small forage species that successfully prevent larger predatory species from ever becoming abundant through impacts on juvenile survival of the predatory species? If depensatory effects are common, they must not be so strong as to entirely prevent large predatory species from invading ecosystems, at least when there is no fishing.

At least four factors likely mitigate against very strong depensatory effects: (*i*) niche specialization, (*ii*) limitation of predation impacts in forage species via risk-sensitive behaviors by the forage species, (*iii*) diffuse predation impacts that act to prevent strong population responses by forage fishes, and (*iv*) spatial propagation effects. Niche specialization is an obvious possibility: successful large predatory species may be ones whose juveniles are competent at acquiring particular food resources, relative to forage fish competitors (i.e., competition may not be all that severe). In terms of the graphical model in Fig. 2, such niche specialization would imply a "failure" in Fig. 2*b*: juvenile foraging time not increasing with increases in abundance of forage species competitors.

The second and third factors involve mitigation of the forage fish numerical response to predator abundance, i.e., a less dramatic response than shown in Fig. 2*a*. If the forage fishes have severely restricted habitat use/foraging activities

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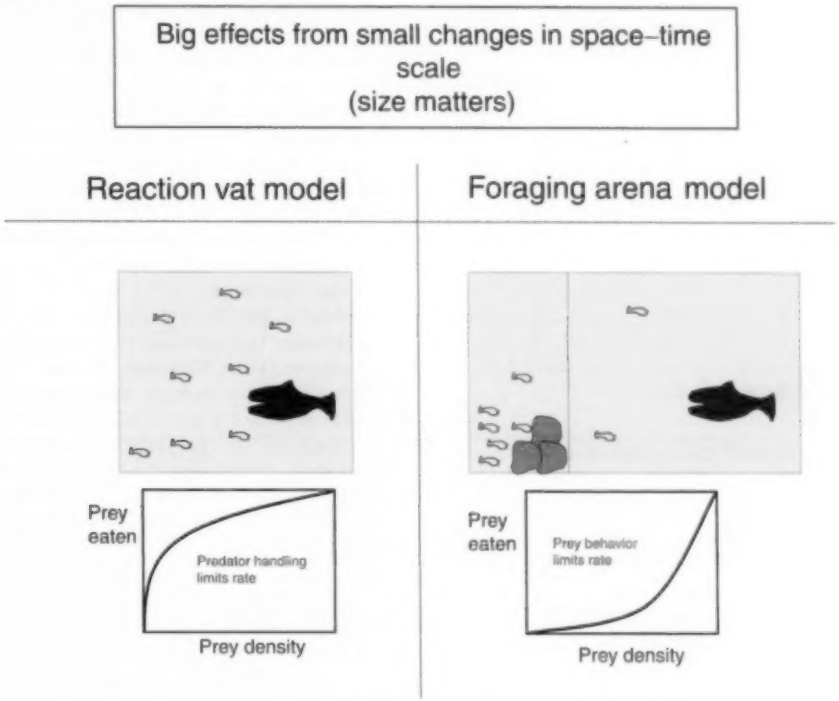
Fig. 4. Risk-sensitive behaviors by juvenile fish imply a deep reversal of predictions about predation impact. Small increases in the space–time scale of experimentation and modeling can result in a reversal in form of the functional response observed, from a type II response for a reaction vat experiment to type III for an experiment where prey can hide from predators unless prey density is high enough to force the prey to spend more time foraging.



due to predation risk in general (risk-sensitive foraging), they may simply not be limited in abundance in the first place by the predatory species in question. In fisheries terms, their natural mortality rate M and (or) recruitment may not be sensitive to changes in abundance of any particular predator that might be reduced through fishing. Alternatively, any temporary increase in their abundance (due to a decrease in their mortality rate) may be reversed by numerical responses of a variety of other predators (diffuse predation impacts).

In physically large ecosystems with a diversity of habitats, juveniles of large predators may find refuges for persistence in particular sites where predation/competition effects are relatively weak. Such sites may then act as "epicenters" for spatial population expansion, as adults produced from the centers gradually move in enough numbers to other sites so as to generate cultivation effects in these sites. That is, cultivation effects may be critical in the range expansion/contraction dynamics often observed for large fish populations (MacCall 1990).

We likewise would not expect strong cultivation/depensation effects for species that show large-scale ontogenetic habitat shifts (large physical separation between juvenile nursery areas and adult feeding areas), possible mainly in marine ecosystems. In cases like anadromous salmon, it is difficult to see how adults could have much direct effect on competition/predation conditions faced by juveniles (although they may have other indirect effects such as fertilization of rearing areas with carcasses).

It should be noted that large ecosystem size per se does not imply that predation/competition effects should be weaker because predation is more "dilute," as suggested by Verity and Smetacek (1996) to explain differences between freshwater and marine systems. Since interactions can be spatially patchy (highly localized) in both environments, it is irrelevant that average densities of predators are much lower in the ocean environment.

Examples?

The most obvious examples of apparent cultivation/depensation effects have been in freshwater ecosystems. There has long been a concern about how to establish "balance" in centrarchid communities, which have a nasty propensity to shift toward dominance by stunted sunfish populations when basses are heavily exploited (Swingle 1950*a*, 1950*b*; Hackney 1979; Olson 1996). In these systems, it is obvious how sunfish forage species impact recruitment of bass via both competition and direct predation. There is a south–north cline toward increasing risk of sunfish dominance to the north, most likely related to the impact of growing season length and the duration of the competition/predation window faced by juvenile basses.

Under heavy exploitation, walleye (*Stizostedion vitrium*) populations in Alberta, Canada, have shown persistent recruitment failure, accompanied by dramatic increases in minnow populations that are thought to prey heavily on walleye larvae (M. Sullivan, Alberta Department of Natural

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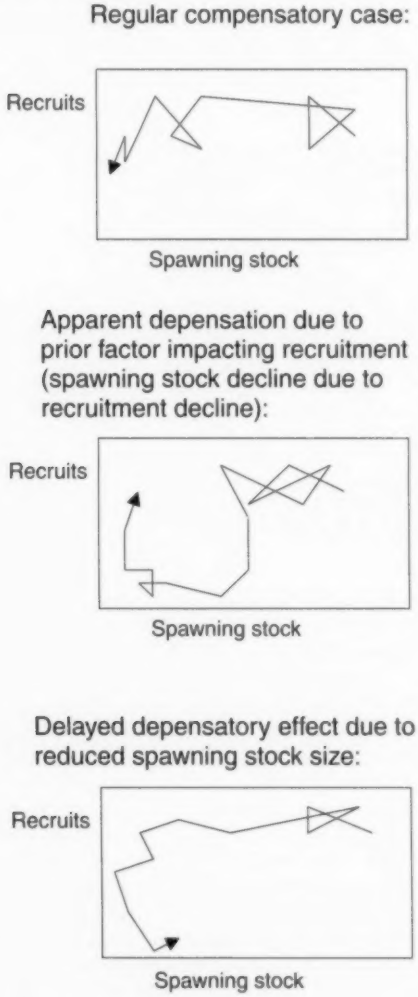
Fig. 5. Patterns in stock–recruitment data expected under alternative hypotheses. In the regular compensation case, juvenile survival rate increases smoothly as spawning stock size decreases. In the apparent (prior) depensation case, recruitment decline precedes (and causes) the spawning stock decline, giving the appearance of depensation unless enough observations are available for the recovery portion of the recruitment "hook." In the delayed depensation case, recruitment may remain high as the stock declines and then finally collapse.


Regular compensatory case:
Recruits
Spawning stock
Apparent depensation due to prior factor impacting recruitment (spawning stock decline due to recruitment decline):
Recruits
Spawning stock
Delayed depensatory effect due to reduced spawning stock size:
Recruits
Spawning stock

Resources, Edmonton, Atla., personal communication). Similar walleye recruitment failures may have occurred in Wisconsin lakes, and walleye have not become established in some lakes with apparently excellent habitat and forage conditions (D. Beard, Wisconsin Department of Natural Resources, Madison, Wis., personal communication). However, most Wisconsin lakes have maintained strong recruitment despite heavy fishing (e.g., Escanaba; Hansen et al. 1998). The striking difference between these regions supports the possibility mentioned above that "diffuse predation" may prevent delayed depensatory effects: Alberta lakes lack the centrarchids (basses, sunfish) that are prominent in the littoral zones of most Wisconsin Lakes.

The northern (2J3KL) Atlantic cod (*Gadus morhua*) stock off Newfoundland showed declines in apparent juvenile survival rate (recruits per spawning biomass) and also body growth rate during the 1980s, following severe stock reduction during the 1970s (Myers et al. 1996; Anderson and Dalley 1997; Shelton and Healey 1999). That stock has not recovered as expected following fishery closure in 1992, and in particular, there is little evidence of recruitment to the larger, offshore migratory component of the stock. If the cultivation/depensation hypothesis applies in this case, it should be possible to demonstrate substantial increases in some smaller species that are competitors/predators on juvenile cod in nursery areas and were preferred prey of adult cod (note that "preferred" is in the technical sense: a high proportion in the diet compared with the proportion in the environment). One possible candidate species is Arctic cod (*Boreogadus saida*). However, note that for the 10 North Atlantic cod stocks that have undergone severe decline (80% or more) in recent years, 6 have not shown the survival decline predicted by the cultivation/depensation hypothesis (Myers et al. 1996). Bax (1998) suggested that predation on juvenile cod by clupeids could exaggerate fishing effects and help lead to a "planktivore-dominated" ecosystem in the Baltic.

The large number of stock–recruitment data sets assembled by Myers and colleagues (Myers et al. 1995*a*, 1995*b*, 1999; www.mscs.dal.ca/~myers/data.html) provides an opportunity to broadly examine the frequency of occurrence of depensatory effects. Because we were concerned about possible transitory and delayed effects that might not be detected by simply fitting stationary stock–recruitment curves to the data (Fig. 5), we had three independent scientists examine the data sets and provide a visual assessment of whether delayed depensation might be present. Of 330 stock–recruitment data sets excluding anadromous salmonid cases, we found (Table 1) that 44–112 could be interpreted as showing some sort of depensatory response, but these represent almost a third of the cases where there are observations at relatively low (20% or less of maximum) spawning stock sizes. Liermann and Hilborn (1997) also suggested that these data sets might contain more examples of depensation than were detected by Myers et al. (1995*a*, 1995*b*). However, only a small number (17–45) of these possible depensatory cases show the delayed response expected under the cultivation/depensation hypothesis, characterized by a downward "hook" (Walters 1987) in the stock–recruit time series (Fig. 5). Far more common, especially for clupeoids, are hooks of the reverse shape where recruitment initially declines, then the spawning stock declines, and then recruitment begins to recover; these cases should not be interpreted as evidence for depensation. Fisheries scientists have generally interpreted these cases as "bad luck": poor environmental conditions leading to recruitment failure, and persistence of the poor conditions for at least some time following implementation of measures aimed at protecting spawning stocks. While such cases might be due to trophic effects (e.g., increase in predators leading to recruitment decline and then predator collapse allowing recruitment to recover; likewise for food supply

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Table 1. Visual characterization of 330 worldwide stock–recruit data sets assembled by Myers and colleages, exlcuding anadromous salmonid cases.

Taxonomic group	No evidence	No depensation	Possible depensation	
			Prior	Delay
Classification by three scientists of data at www.mscs.dal.ca/~myers/data.html				
Clupeiformes	24–32	11–23	14–25	3–7
Gadiformes	36–52	6–18	6–15	7–14
Perciformes	38–47	6–17	1–10	2–11
Pleuronectiformes	27–30	1–11	1–7	1–3
Salmoniformes	16–19	11–16	3–4	2–5
Miscellaneous	11–22	3–8	2–6	2–5
Total	152–202	38–93	27–67	17–45
Classification by Walters of data in Myers et al. 1995*a* and 1995*b*				
Clupeiformes	21	28	3	2
Gadiformes	36	18	4	11
Perciformes	12	5	2	1
Pleuronectiformes	21	7	2	0
Salmoniformes	2	3	1	2
Miscellaneous				
Total	92	61	12	16

Note: Ranges are for three independent scientists. "No evidence" means no observations at low enough spawning stock size (<20% of maximum) to expect depensatory effects, "no depensation" means recruitment relatively high at lowest stock sizes and (or) an upward hook in the recruitment time series, and "possible depensation" means at least a few observations of relatively low recruitment per spawner (juvenile survival rate) at low stock size. In depensation cases, "prior" means that survival decline preceded stock decline, suggesting an agent other than delayed depensation likely responsible for apparent depensation.

dynamics), we would not interpret them as evidence for persistent depensatory effects, delayed or otherwise.

The taxonomic distribution of possible depensation cases in the Myers and colleagues database (Table 1) provides direct support for using foraging arena assumptions in ecosystem models and recruitment analysis (Figs. 3 and 4). Were predator–prey interactions mainly of the mass action or reaction vat functional form, we would expect depensation effects to be most common in taxonomic groups dominated by smaller "forage" species (Clupeiformes fishes) and least common in groups dominated by piscivores (Gadiformes fishes). In fact, we see the opposite: the incidence of depensatory cases is highest in Gadiformes fishes, and the two delayed depensation cases in Salmoniformes fishes are for a large piscivore (northern pike (*Esox lucius*) in the two basins of Lake Windermere, Great Britain). This is just what we expect from foraging arena theory, assuming that there has been strong selection in smaller species for distributional/behavioral tactics to limit predation risk. Also, we generally predict unrealistically violent predator–prey oscillations in Ecosim models and unrealistically large temporal variation in natural mortality rates of forage species unless we assume such tactics.

It is likely that available stock–recruitment data sets provide an underestimate of the risk of cultivation/depensation effects. Most of the data have been collected since the middle of the twentieth century, and many stock collapses due to depensatory effects could have occurred much earlier in world fishery development so that what we have left to study today are mainly the most productive and resilient stocks. It is not unusual to hear laments by older, experienced fisheries observers about the disappearance of various species and stock components, before anyone had the time or resources to study them. Data collected for research purposes are typically among the last things to occur in the developmental sequence of most fisheries. On an even longer time scale, the patterns of mortality imposed by the industrial fisheries of this century are unlike anything in the evolutionary history of most fish species (Frank and Leggett 1994).

Implications for harvest management and research

The arguments presented in this paper imply need for a very particular third step in the evolution of the theory of fishing. The first step in this evolution was the development of simple catch–effort relationships (Baranov, Graham, Scahefer, Gulland) that did not explicitly use any ecological variables for prediction; this approach "worked" in a world of slow fisheries development that did not cause either rapid population size/structure transients or severe depletion. The second step, heralded by Schaefer's (1957) method for fitting logistic population models to time series data, was to recognize population size and structure as dynamic variables. Most of the elaborate machinery of modern fisheries assessment has really just added detail to the population state representation and statistical analysis, allowing better interpretation of data from rapidly changing populations under modern, more violent exploitation regimes. It is noteworthy that we generally do not obtain much better fits to population time series data (or predictions of harvest impact) with the elaborate models than we can with simple logistic or delay-difference models; the really big step was to recognize population size as a critical state variable. Single-species models served us well until very severe stock depletions began to occur.

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We argue that in this "new" domain of fisheries system states, where severe depletions and risk of recruitment overfishing are common, that the single-species recruitment models are no longer reliable. While we understand and agree with the call for an "ecosystem approach" to fisheries management (Mooney 1998), we also recognize that this approach is complex and will require a substantial effort before successes can reinforce its value. In the interim, we believe that we must at least try to extend the theory of fishing so as represent some other, particularly important variables (predators/competitors of juvenile fish) in order to predict the pathological dynamics that sometimes accompany severe depletion. That is, we need to take a third basic step toward inclusion of more variables in predictive models, but in a very particular way. Just as population dynamics modelers had much of the modeling and statistical machinery already available when they began the step into modern stock assessment, so do we have the machinery largely in place to begin the next step, via ecosystem analysis tools like multispecies virtual population analysis (Pope 1991; Sparre 1991) and Ecopath/Ecosim (Walters et al. 1997, 2000).

As for any depensatory mechanism, the primary policy implication of cultivation/depensation effects is the existence of a critical population size, defining a division between two qualitatively different domains of population behavior. In the high-abundance domain, traditional single-species assessment procedures and prescriptions should work reasonably well. But should abundance be driven into the lower domain, we expect to see accelerating population collapse toward some low equilibrium or extinction. Reduction in exploitation rates after entering this domain may or may not allow recovery, depending in a quite unpredictable way on the *quantitative* details of how the juvenile survival rate is impacted.

Can we say anything in general about the probability of there being such a critical population size, or what this size might be relative to reference points like unfished abundance? We think not: the development of depensatory effects as population size is reduced depends on the quantitative pattern of forage (competitor/predator) response, i.e., the specific form of the numerical response in Fig. 2*a*. Models like Ecosim II can be used to define a range of possible responses, depending on assumptions about factors ranging from predator feeding rates to behavioral characteristics of the forage fish that may limit their vulnerability to predation. But the parameters that define the "correct" response obviously cannot be estimated reliably from historical data where the response is not yet evident, and these parameters summarize a very complex set of direct and indirect impacts of predation (Bax 1998). Comparative analysis of stock–recruitment data (Table 1; Myers et al. 1995*a*, 1995*b*; Liermann and Hilborn 1997) hints that at least some delayed depensation effects may occur in up to 10–20% of severely overfished cases. But the available data sets do not have enough observations at low stock sizes to make a convincing quantitative case about risk. We suspect that 10% may be a considerable underestimate of the risk for freshwater piscivores and possibly also for larger marine piscivores (particularly Gadiformes). We note, too, that many of the data sets in hand derive from populations that are components of multispecies fisheries. Therefore, the observed responses to exploitation include some degree of ecological change greater than that of simple mortality rates for single stocks. Ecosim may be a particularly valuable tool in evaluating those mixed impacts.

From a biological perspective, we might be willing to treat relatively rare instances (e.g., 10–20% of stocks; Table 1) of delayed depensation as biological curiosities rather than a matter for considerable research investment. But from a social and economic perspective, a 10% risk of stock collapse and (or) delayed recovery can be a very serious matter, especially where a substantial community of people is deeply dependent on the stocks. Would any fishery manager in Canada be willing to step forward and admit to having knowingly accepted a 10% chance that the Newfoundland cod stocks would collapse and show long delays in recovery? We think not, and we conclude from such examples that the risk should be taken very seriously indeed.

Depensation and physical "environmental effects" may interact, making prediction of critical population size even more difficult (Collie and Spencer 1993). Physical changes that impact productivity and size of juvenile nursery areas may move the response curves in Fig. 2 in complex ways, depending on the details of how both juveniles and their competitors/predators are impacted. Outcomes can range from mitigation of effects if there is a differential negative effect on the other species to severe reinforcing of negative effects if the other species are differentially enhanced. Indeed, the cultivation/depensation hypothesis offers an explanation for why correlations between recruitment and environmental factors are so prone to break down over time (Drinkwater and Myers 1987; Myers et al. 1997). Strong immediate responses to physical change are likely to be followed by dampening of the effect as trophic structure adjusts to the change.

If we cannot predict the critical population size in advance, what might we monitor in order to provide the earliest possible management reaction should depensatory effects start to develop? Here there are two obvious recommendations. First, develop survey methods to provide direct, immediate measures of juvenile survival rate and recruitment performance. Age-structured methods based on surveys and harvest of older fish do not provide reliable recruitment/survival estimates for each cohort until that cohort has been in the fishery for at least a few years. Second, also develop survey methods (or use the juvenile survey methods themselves) for abundance trends of a suite of potential competitor/predators in major juvenile nursery and rearing areas. In these surveys, routinely monitor diet compositions of juveniles and these species. Although multispecies surveys may fail to detect potential depensatory effects if such effects occur in concentrated space–time windows (e.g., seasonal impact on a particular size range of juveniles), their failure is the essential next step toward discovering this type of "critical period" or "bottleneck" effect.

As of 1990, assessments based on goals such as $F_{0.1}$, along with general belief that recruitment is poorly correlated with spawning biomass, led to a common view that the spawning biomass for most fish can be safely reduced at least 60–80% from natural levels without a substantial risk of recruitment failure. This view has been strongly challenged in the last decade (Mace 1994; Myers et al. 1994),

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thanks particularly to the comparative recruitment studies by Myers and his colleagues along with empirical studies of long-term population change (Patterson 1992). It is now rare to see suggestions that spawning biomass can be safely reduced by more than 60–70%. We suggest that even these more conservative goals are based on very limited temporal experience with initial recruitment responses to stock size reduction and over the long term may be dangerously optimistic. To insure against lagged depensation effects, we suggest that spawning stock abundance goals should generally be no less than 50% of unfished spawning biomass, which in any case should usually produce yields not much less than at the more dangerously low levels (e.g., 30%) often recommended.

Where is the burden of proof?

Ecosystem models have drawn considerable criticism from proponents of single-species assessment methods. Ecosystem models have not been "proven" to work and have not been "tested" by fitting them to available time series data, they have many parameters whose effects are not easily seen in the data, and there is no proof that representations of species interaction effects are really necessary for policy formulation (e.g., see Hilborn and Walters 1992, p. 448: "We believe that the food web modeling approach is hopeless as an aid to formulating management advice"). In short, defenders of single-species assessment have argued that (*i*) you cannot do it and (or) (*ii*) we do not need it. We think that these arguments are deeply misleading and in fact represent a bizarre reversal of the burden of proof: what really demands justification is not attempts to understand consequences of trophic interactions but rather continuing the pretense that we can get away with not doing so!

Consider the "you cannot do it" argument. By appropriate choice of vulnerability parameters in functions for predicting predation mortality rates and foraging time/predation risk responses (e.g., Ecosim eq. A3, Appendix), we can turn ecosystem models into a collection of "independent" single-species models with essentially the same response dynamics as the single-species models now used for most assessment. If we then follow the standard assessment practice of including many nuisance parameters to account for unexplained recruitment variation ("process errors," "recruitment anomalies"), we can then fit these population "submodels" just as well as we can fit their single-species analogs and make the same predictions about policy parameters like maximum sustainable yield. If we then vary parameters so as to strengthen trophic interaction effects, we are almost bound (given many covarying time series) to "explain" at least some of the variation initially attributed to nuisance parameters. Such exercises prove nothing (correlations could be spurious), just as do exercises showing that recruitment anomalies are correlated with environmental factors. At this point, ecosystem model predictions about impacts of extreme abundance changes and impacts of policy changes such as fishing at the bottom of the food chain will begin to depart from the predictions of single-species models. Should we trust such predictions? Of course we should not, any more than we should trust the predictions of single-species assessments: the only "proof" is to see which predictions stand the test of time, and we cannot obtain such proof if we resist making the predictions in the first place.

It is even more misleading to argue that we do not "need" ecosystem models. Most of the apparent success of single-species assessment approaches has come from three tactics employed by experienced assessment scientists like the senior author. First, we take considerable care in choice of case populations and data sets to use as test cases in reporting methods development, when possible avoiding uninformative and (or) perverse data sets (which in fact make up a clear majority in the Myers synthesis of stock–recruitment data sets). Second, we shrug off much of the interesting variation, by calling it "anomalies" or "environmental effects," saying only that we need to perform risk assessments under various alternative hypotheses about future patterns of variation. This tactic leads us directly away from recognizing serious policy issues such as the risk of delayed depensation. Third, we restrict ourselves to asking only the most menial of policy questions, and in this, we do deep disservice to fisheries management by encouraging the use of correspondingly myopic policy approaches (e.g., my model cannot tell you anything about the efficacy of marine protected areas because it does not account for the spatial and trophic effects of such a policy, so let us talk about next year's allowable catch instead). Assessment scientists who use these tactics may soon find themselves left behind by both the science and fisheries decision-making.

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Appendix. "Foraging arena" concept as represented in Ecosim

In trophic models, we need to predict consumption rates Q_{ij} of prey types i by predator types j. Suppose that at some moment in time the total prey population is N_i and the total predator population is N_j. Simple reaction vat or mass action encounter models predict Q_{ij} from encounter rate arguments as $Q_{ij} = a_{ij}N_iN_j$ or as $Q_{ij} = f(N_i)N_j$, where $f(N_i)$ is the predator functional response to overall prey density. But in reality, if we look at any collection N_i of prey, we will find these individuals at any moment to be in a wide variety of "vulnerability states" with respect to N_j, depending on spatial position (e.g., in hiding places) and activity (e.g., resting versus actively feeding). Ecosim attempts to model this vulnerability distribution by treating the prey as being in one of two behavioral states, "invulnerable" and "vulnerable," with exchange between these states possibly representing both behavioral and physical mixing processes. Animals in the vulnerable state are said to be "in the foraging arena for i–j interaction," and we assume that there are V_{ij} of these at any moment. The dynamics of V_{ij} are modeled as having three components: (1) movement of individuals into the vulnerable (foraging arena) state at rate $v_{ij}(N_i - V_{ij})$, (2) movement of individuals out of this state at rate $v'_{ij}V_{ij}$, and (3) consumption of vulnerable individuals at mass action rate $Q_{ij} = a_{ij}V_{ij}N_j$. Note that we ignore predator handling time/satiation in the attack rate component 3, following the observation that predators with full stomachs are not a common field observation (D. Schindler, Department of Zoology, University of Washington, Seattle, Wash., unpublished data). We then assume that the dynamics of V are very fast compared with the dynamics of the Ns, so V quickly adjusts so that the three rates 1–3 remain near balance (dV/dt stays near zero). This variable speed-splitting assumption (similar to speed-splitting arguments used to derive classic type II functional response equations from handling time considerations) leads to the prediction

$$(A1) \quad V_{ij} = v_{ij}N_i/(v_{ij} + v'_{ij} + a_{ij}N_j).$$

Combining this prediction with assumption 3 above leads to

$$(A2) \quad Q_{ij} = a_{ij}v_{ij}N_iN_j/(v_{ij} + v'_{ij} + a_{ij}N_j).$$

This model implies Q_{ij} proportional to N_i and saturating in N_j (Fig. 3). In traditional predator–prey terminology, the denominator term $a_{ij}N_j$ represents a "ratio dependence" or localized "predator interference competition" effect. From eq. A2, instantaneous prey mortality rate Z_{ij} due to predator j is predicted to vary as

$$(A3) \quad Z_{ij} = Q_{ij}/N_i = a_{ij}v_{ij}N_j/(v_{ij} + v'_{ij} + a_{ij}N_j).$$

That is, Z_{ij} is not simply proportional to predator abundance but rather increases asymptotically toward maximum rate v_{ij} as predator abundance increases; for low v_{ij} and high predator search rate a_{ij}, Z_{ij} is predicted to be nearly constant (constant natural mortality M assumption).

In Ecosim, we allow users to introduce additional variation into predation mortality rates Z_{ij} by assuming changes in v_{ij} due to intraspecific competition among prey i and risk-sensitive behavioral responses. We monitor simulated food consumption rates by N_i and increase/decrease v_{ij} as feeding rate decreases/increases; the "target" feeding rate can be made inversely proportional to predation risk per time foraging. A basic implication of these time adjustment hypotheses is that for fixed predator abundance (all N_j constant) and N_i representing juveniles of some fish species, Z_{ij} will vary linearly with N_i so as to produce the widely observed Beverton–Holt form (flat-topped) of stock–recruitment curve (Walters and Korman 1999).

We see four common mechanisms that can decrease the vulnerability parameters v_{ij} so as to create stabilizing effects (Abrams and Walters 1996) and the appearance of "ratio-dependent" or "bottom-up" control of consumption rates (Q_{ij} limited to maximum $v_{ij}N_i$ no matter how many predators are present).

(1) Risk-sensitive prey behaviors

Prey may spend only a small proportion of their time in foraging arenas where they are subject to predation risk, otherwise taking refuge in schools, deep water, littoral refuge sites, etc.

(2) Risk-sensitive predator behaviors (the "three to tango" argument)

Especially if the predator is a small fish, it may severely restrict its own range relative to the range occupied by the prey, so that only a small proportion of the prey move or are mixed into the habitats used by it per unit time; in other words, its predators may drive it to behave in ways that make its own prey less vulnerable to it.

(3) Size-dependent graduation effects

If N_i represents an aggregate of different prey sizes, and predator j can take only some limited range of sizes, v_{ij} can represent a somewhat slower process of prey graduation into

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and out of the vulnerable size range due to growth. Size effects may of course also be associated with distribution (predator–prey spatial overlap) shifts.

(4) Passive, differential spatial depletion effects

Even if neither prey nor predator shows active behaviors that create foraging arena patches, any physical or behavioral processes that create spatial variation in encounters between i and j will lead to local depletion of i in high-risk areas and concentrations of i in partial predation "refuges" represented by low-risk areas. "Flow" between low- and high-risk areas (v_{ij}) is then created by any processes that move organisms.

These mechanisms are so ubiquitous that any reader with aquatic natural history experience might wonder why modelers have ever chosen to assume mass action, random encounter models (or infinite v_{ij}) in the past.

For readers who might think it practical to avoid simplifications like eqs. A1 and A2 by explicitly modeling the full space–time structure of individual predator–prey encounters, be warned that the foraging arena structure arises from biology and physics operating at very small scales indeed. Foraging and movement dynamics generally take place at time scales of minutes to hours and involve complicated spatial movements at scales of a few metres to a few hundred metres. Indeed, it is probably because we have not thought carefully about heterogeneity at these very difficult scales that we have been willing to use mass action models in the past. Note further that just complicating the trophic model state representation by including details of size structure and macroscale spatial overlaps of predators and prey (e.g., Stefansson and Palsson 1998) does not solve the microscale representation problem at all and could still be completely misleading if only simple mass action interaction rates are used in the detailed calculations.

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Fishing down Canadian aquatic food webs[1]

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Abstract: The mean trophic level (TL) of fish landed in fisheries on the east and west coasts of Canada is declining by 0.03–0.10·decade^{-1}, similar to global trends. This finding is based on data from United Nations Food and Agriculture Organization and the Canadian Department of Fisheries and Oceans and other Canadian sources for the period 1873–1997. Significant rates of decline in mean TL were obtained even when key species — Atlantic cod (*Gadus morhua*) on the east coast and Pacific herring (*Clupea pallasi*) and Pacific hake (*Merluccius productus*) on the west coast — were omitted from the analysis. Fish taken in inland water fisheries did not exhibit a decline in mean TL. Two models were developed, based on length and age, respectively, for correcting TL estimates of individual species for the effects of changes in body size due to changes in fishing mortality. Both produced corrections that were small relative to changes in mean TL that resulted from changes in species composition of the catch over time. Overall, these results suggest that the mean TL of fish landed can be used as an index of sustainability in multispecies fisheries and that its reliability will depend on the quality of the data and length of the time series available for analysis.

Résumé : Le niveau trophique (NT) moyen des poissons débarqués dans les pêches des côtes est et ouest du Canada baisse de 0,03 à 0,10 par décennie, comme c'est le cas dans les tendances mondiales. Ce constat se fonde sur des données de l'Organisation des Nations Unies pour l'alimentation et l'agriculture (FAO), du ministère des Pêches et des Océans du Canada et d'autres sources canadiennes, pour la période allant de 1873 à 1997. Des taux significatifs de déclin du NT moyen ont été obtenus même lorsque des espèces clés — morue franche sur la côte atlantique, hareng et merlu sur la côte pacifique — étaient omises dans l'analyse. Les poissons capturés dans les eaux intérieures ne présentaient pas de baisse du NT moyen. Deux modèles ont été construits, basés respectivement sur la longueur et sur l'âge, pour corriger les estimations du NT de chaque espèce de façon à tenir compte des effets des changements de la taille corporelle dus à des changements dans la mortalité par pêche. Les deux modèles ont produit des corrections qui étaient petites par rapport aux changements dans le NT moyen dus à des modifications de la composition spécifique des captures au fil du temps. Globalement, ces résultats permettent de penser que le NT moyen des poissons débarqués peut être utilisé comme un indice de durabilité dans les pêches plurispécifiques, et que sa fiabilité dépendra de la qualité des données et de la longueur des séries chronologiques disponibles pour les analyses.

[Traduit par la Rédaction]

Introduction

There is broad agreement in the literature that fisheries affect not only target and bycatch species but also the ecosystems in which these species are embedded (Parsons 1996; National Research Council 1999). The resulting calls for ecosystem-based management are more controversial. One reason is because there is at present no consensus on possible ecosystem "reference points" analogous to those used for single-species management, such as maximum sustainable yield or $F_{0.1}$.

One recurrent feature of aquatic ecosystems exploited by modern fisheries is the tendency for the biomass of large, long-lived, often piscivorous species to decline more rapidly than that of smaller, shorter-lived, often zooplanktivorous species (Kirkwood et al. 1994; Jennings et al. 1997; National Research Council 1999), a feature related to the usually low natural mortality of the former group (Myers and Doyle 1983). Therefore, where fleets target both large and small fishes (or use unselective gear), the contribution of fishes from the lower part of the food web to the aggregate catches will tend to increase over time. This was confirmed by the recent demonstration of a decline in the mean trophic level (TL) of organisms (fishes and invertebrates) landed globally by fisheries (Pauly et al. 1998).

Thus, the mean TL of organisms in landings from a given ecosystem could be used to integrate a vast array of biological features pertaining to the species therein, and its continuous decline, if associated with stagnating or declining catches, interpreted as indicating lack of sustainability at the ecosystem level (because overall biological production is highest at low TL; Pauly and Christensen 1995). This agrees

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with Caddy (1998) who suggested that "multispecies reference points could be derived from ecological/food web models."

However, if it is to become accepted as an index of the impact of fisheries on ecosystems, mean TL will have to be shown to be applicable in a variety of national settings, with a wide range of underlying statistical data, resource types, and fisheries. Also, issues of model sensitivity must be addressed, notably regarding the within-species changes of TL due to the change in size composition caused by fishing. We present such an evaluation here based on the mean TL of organisms in the landings of fisheries on the east coast (Maritimes, Quebec, and Newfoundland–Labrador), on the west coast (British Columbia), and in inland waters (lakes and rivers) of Canada. Two new models are developed for the quantitative assessment of the effects of size changes on the estimation of mean TL values.

Materials and methods

Catch/landings statistics

East coast

The landings data used for the east coast of Canada cover the period 1950–1997 and were supplied by the Government of Canada to the Food and Agriculture Organization (FAO) of the United Nations (www.fao.org) (similar FAO data sets were used in association with other sources for the west coast and inland waters of Canada). This data set, comprising 72 statistical categories that range from species (50) to genera (10) and higher groups (12), consists mainly of reports by or to Canadian authorities. These data do not include all the catches of distant-water fleets based in Europe, which fished until the 1970s in what subsequently became the Canadian Exclusive Economic Zone. Key features of this data set are provided in Table 1.

West coast

Statistics from a variety of sources were used to estimate the catches of the commercial fishery in British Columbia from 1873 to 1996. FAO statistics commenced in 1950. Annual reports to Ottawa from the Inspector of Fisheries for British Columbia commenced in 1873 and were published in "Canada Sessional Papers" by the Dominion Bureau of Statistics from 1919 to 1970. From 1952, landings data were also published in "British Columbia Catch Statistics." For some species, review articles were available that summarize commercial landings and provide factors for conversion from nonmetric units (Table 2).

Recreational catch statistics (for salmon) started in 1953; estimates for other species such as lingcod (*Ophiodon elongatus*) and rockfish are included in the annual recreational surveys only from 1981. Aboriginal salmon catches have been recorded by the Canadian Department of Fisheries and Oceans (DFO) since 1951. Minimum estimates of aboriginal catches for 1873–1950 were derived from Argue et al. (1990) and from estimates of precontact seafood consumption by First Nations (Hewes 1973).

The series of mean TLs constructed from these data exhibited strong fluctuations. We identified the simplest set of piecewise polynomials that would adequately describe the data using the algorithm described in Hintze (1998).

Inland waters

The freshwater landings data used here included FAO statistics (1950–1997) complemented by records for 1917–1968 collected by the Dominion Bureau of Statistics in collaboration with federal and provincial fisheries departments, records for 1969–1974 collected by Statistics Canada, records for 1976–1989 collected by the DFO (available online: www.dfo-mpo.gc.ca/communic/statistics/stat_e.htm), and records for 1990–1997 collected by DFO Statistical Services, Ottawa.

For the inland waters data set, we excluded marine fishes caught in estuarine waters, notably Atlantic cod (*Gadus morhua*), Atlantic herring (*Clupea harengus*), and rainbow smelt (*Osmerus mordax*). Landings in the early twentieth century were reported as either raw or finished products and in imperial units, e.g., fresh, salted, or in oil, as barrels, cases, pounds, or hundredweights. Conversions to metric equivalents were performed using factors in the fisheries reports for 1947 and 1948 of the Dominion Bureau of Statistics. Species names from various sources had to be matched, as some species were not reported or were given different names in different years. The combined time series of inland water landings included only those species for which continuous data were available (Table 3).

TLs

The TL estimates used here all rely on diet composition data and on the equation

$$(1) \qquad TL_i = 1 + \sum_{j=1}^{n} DC_{ij}\, TL_j$$

where i is the predator, j the nth prey, and DC_{ij} is the diet composition, expressing the fractions of each j in the diet of i. Assignment of TL starts with plants and detritus, both with a definitional TL value of 1. Thus, a consumer eating 40% plants (TL = 1) and 60% herbivores (TL = 2) will have a TL of $1 + (0.4 \times 1 + 0.6 \times 2) = 2.6$.

The variance of the TL estimates from eq. 1, referred to here as the omnivory index (OI), is calculated from

$$(2) \qquad OI_i = \sum_{j=1}^{n} (TL_j - TL_{preys})^2\, DC_{ij}$$

where TL_{preys} is the average TL of the n prey species of i and the other terms are as defined in eq. 1. We also use the standard error of TL, defined as the square root of the corresponding OI, for the catch pyramids described below.

The DC_{ij} and TL_j used here were obtained from two related sources: (1) mass-balance trophic models of ecosystems of the east and west coasts of Canada or adjacent areas, constructed with the ECOPATH software (Christensen and Pauly 1992; www.ecopath.org), and (2) published, species-specific diet composition data (for the DC_{ij}) and previous (ECOPATH-based) estimates of the corresponding TL_j, as incorporated in the "Food items table" of FishBase (Froese and Pauly 1998).

TL estimates obtained using source 1, pertaining to species or higher taxa, corresponded closely to independent estimates of TL assessed using stable isotope ratios of nitrogen from Prince William Sound, Alaska (Kline and Pauly 1998). Herein, use was made of the observation that for every link in a food chain, the concentration in animal tissues of the heavier isotope (^{15}N) increases by a nearly constant percentage (≈3.4%) relative to that of ^{14}N. This suggests that TL estimates based on source 2 should also be reliable. The TL estimates of major species are summarized in Tables 1–3. Details of these and TL estimates for the other species considered in our analyses are documented in FishBase (Froese and Pauly 1998, with updates on www.fishbase.org).

Mean TLs of organisms in fisheries landings were calculated for each year using

$$(3) \qquad \overline{TL}_k = \sum_{i=1}^{m} Y_{ik}\, TL_i \,/\, \sum_{i=1}^{m} Y_{ik}$$

where Y_{ik} is the landings of species i in year k and TL_i is its TL.

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Table 1. Key features of the data set used for analyzing Canadian east coast fisheries (1950–1997)[a] (also see Fig. 3A).

Group[b]	Groups/species included (TL)[c]
Molluscs	More than eight species of clams, mussels, oysters, quahogs, and scallops (2.1); northern shortfin squid (3.2); longfin squid (3.3)
Flatfishes	American plaice and witch flounder (3.1); flatfish nei (3.2); winter flounder, yellowtail flounder, and Greenland halibut (3.5); Atlantic halibut (4.5)
Other invertebrates	11 groups (about 30 species) from sea urchins and snow crabs (2.3)[d] to lobster (2.6)[e]
Other fishes	21 groups (about 100 species) from rainbow smelt (2.6) to swordfish (4.5)
Redfishes, basses, and shads	Sand lances (3.0); alewife (3.1); shad (3.2); wolffishes nei (3.4); lumpfish and angler (3.5); Atlantic redfish (3.6); striped bass (4.6)
Gadoids (excluding cod)	Atlantic tomcod (3.3); Greenland cod (3.5); red hake and haddock (3.6); saithe and roundnose grenadier (3.8); white hake and tusk (4.2); silver hake (4.3)
Small pelagics	Herring (3.1); pelagic fishes nei (3.2); mackerel (3.7)
Atlantic cod[f]	TL = 4.01 (from Bundy et al. 2000)

[a]Detailed spreadsheet available from first author; FAO catches are from FishBase (Froese and Pauly 1998; www.fao.org).
[b]Groups ranked by year at which 50% of cumulative landings occurred (with "most recent" group up) to emphasize species succession; weighted mean TL series based on individual species, not group means.
[c]Nei = FAO term for "not elsewhere identified"; details on TL estimates including sources of diet information and standard errors may be found in FishBase (Froese and Pauly 1998, with updates on www.fishbase.org) and in Bundy et al. (2000).
[d]TL estimate for *C. opilio* from diet composition data in Wieczorek and Hooper (1995) and mean prey TL in FishBase.
[e]TL estimate for *H. americanus* from diet composition data in Elner and Campbell (1987) and mean prey TL in FishBase.
[f]von Bertalanffy growth parameters and mortality for cod: L_∞ = 130 cm total length; W_∞ = 24 400 g; K = 0.12·year^{-1} (May et al. 1965); M = 0.18·year^{-1} (Pinhorn 1975).

Table 2. Key features of the data set used for analyzing Canadian west coast fisheries (1873–1996)[a] (also see Fig. 3B).

Group[b]	Groups/species included (TL)[c]	Fishery	Data source(s)
Miscellaneous invertebrates	13 groups (about 30 species) from bivalves and sea urchins (2.1) to shrimps (2.6)	Commercial and some aquaculture (oysters)	Sessional papers; Elsey 1933
Hake	*Merluccius productus*	Commercial	DFO
Small pelagics	Pacific herring and pilchard (3.0); mackerel (3.3)	Commercial	1884–1937: sessional papers; pilchard (1938–1948): Culley 1971; herring (1938–1950): Hourston 1980
Marine mammals[d]	Harbour seal, miscellaneous whales, and sea lions (4.0); fur seals (4.2)	Commercial	Bigg 1969; Pike and MacAski 1969
Other fishes	17 groups (about 100 species) from smelts (3.0) to halibut (4.0) and tuna (4.2)	Mainly commercial	Sessional papers; Carrothers 1941; Hart and McHugh 1944; Ketchen 1986; Cass et al. 1990; Stocker 1994
Salmonids[e]	Coho, chinook, chum, pink, sockeye salmon, and steelhead trout (3.8)	Commercial	1873–1982: Shepard et al. 1985; Shepard and Argue 1989; 1983–1996: DFO
		Aboriginal	1873–1951: Hewes 1973; Argue et al. 1990; 1985–1994: DFO
		Recreational	1953–1994: DFO

[a]Extracted from detailed spreadsheet available from first and last authors.
[b]Groups ranked by year at which 50% of cumulative landings occurred (with most "recent" group up) to emphasize species succession; weighted mean TL series are based on individual series, not group means.
[c]Details on TL estimates including sources of diet information and standard errors may be found in FishBase (Froese and Pauly 1998, with updates on www.fishbase.org).
[d]Conversion from individual weights: harbour seal, 81 kg (Fisher 1952); northern fur seal skin, 160 kg (Jefferson et al. 1993); Steller sea lion, 535 kg (Schusterman 1981; Bigg 1988); humpback, 40 t; blue, 160 t; sei, 30 t; fin, 75; minke, 14 t; right, 80 t; gray, 35 t; sperm, 57 t; Baird's beaked whale, 12 t (Jefferson et al. 1993).
[e]Conversion from individual weights: coho and chum, 4.52 kg; chinook, 9.05 kg; pink, 1.81 kg; sockeye, 2.71 kg; steelhead trout, 4.52 kg (Argue et al. 1990).

Catch pyramids

The mean TLs estimated from eq. 3 are presented here as temporal trends and as "catch pyramids" that contrast the distribution of landings by TL at the start and end of the FAO time series of landings, i.e., 1950 and 1997. The approach used to construct the catch pyramids uses the standard errors of the TL_j to define triangular distributions (base of triangle = mean TL of each group ± 2 SE) to assign group-specific catches to different TL classes.

Changes of TLs

Caddy et al. (1998), commenting on the "fishing down the food web" approach initially presented in Pauly et al. (1998), pointed out that the TLs of individuals of a given fish or invertebrate species will vary between populations and different periods and especially between different ontogenic stages.

We accommodated nonontogenic variability of TL by concentrating on diet composition data from Canadian ecosystems. How-

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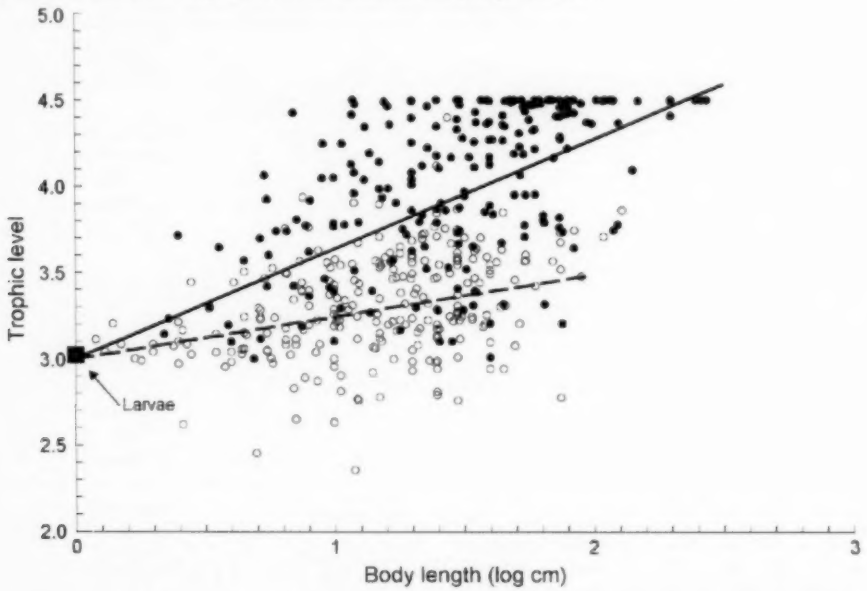
Table 3. Key features of the data set used for analyzing Canadian inland water fisheries (1917–1997)[a] (also see Fig. 3C).

Group[b]	Species included (TL)[c]
Other fish	*Pimephales promelas* (2.1); *Hiodon alosoides* and *Lepomis gibbosus* (3.1); *Ameiurus nebulosus* and *Acipenser fulvescens* (3.3); *Ambloplites rupestris* (3.4); *Anguilla rostrata* (3.6); *Lota lota* (4.0)
Sauger	*Stizostedion canadense* (4.0)
Carp	*Cyprinus carpio* (2.2)
Perch	*Perca flavescens* (3.4)
Salmonids[d]	*Salvelinus fontinalis* (3.0); *S. alpinus* (4.4); *S. namaycush* (4.5)
Cisco	*Coregonus artedi* (3.5)
Sucker	*Catostomus commersoni* (2.6)
Pike	*Esox lucius* (4.5)
Walleye	*Stizostedion vitreum* (4.5)
Whitefish	*Coregonus clupeaformis* (2.9)

[a]Detailed spreadsheet available from first author.
[b]Grouped only for this table and Fig. 3C; weighted mean TL series based on landings and TL of individual species.
[c]Details on TL estimates and standard errors may be found on www.fishbase.org.
[d]Pacific salmon (especially coho and chinook) introduced into the Great Lakes and other freshwater bodies are not included, as biomasses (and hence landings) largely depend on continuous stocking.

Fig. 1. Relationship between TL estimates and body length (cm) in 180 species of fishes. The regression lines (forced through the origin, representing larvae with TL = 3 and length ≈1 cm) have slopes of $b_a = 0.24$ for first-order carnivores (broken line and open circles, representing herring and other small pelagic and demersal fishes) and $b_b = 0.63$ for higher-order carnivores (solid line and solid circles, representing cod-like and other large piscivorous demersal and pelagic fishes).



ever, we could not accommodate between-year variability of TL because suitable time series of diet composition could not be found. Moreover, we believe this form of variability to be small, e.g., a large piscivore cannot revert to feeding on herbivorous zooplankton when prey fishes are scarce. Indeed, feeding habits in fishes are largely a function of morphology and size (e.g., see De Groot 1981).

Ontogenic changes were accommodated by first documenting and quantifying general relationships between the TL and size of fishes. (Data were not available to document such relationships in invertebrates. Thus, we assume here that the TL of invertebrates does not change with fishing mortality. This assumption is briefly revisited in the Discussion.) This was done by first extracting from FishBase those species for which at least two TL values were available, of which one pertained to the adult stage. We found 180 species that met this criterion, represented by 578 TL estimates. In the absence of true herbivores among Canadian fishes, these species were then pooled into two sets: first-order carnivores, i.e., fishes whose adult TL ranges from 2.75 to 3.75, close to the TL = 3 typical of their larvae (which feed almost exclusively on herbivorous zooplankton), and higher-order carnivores, i.e., fishes whose adult TL reaches values higher than 3.75 (Froese and Pauly 1998; Cortés 1999).

Regression lines linking the TL estimates and the corresponding (log) length values of each group were then forced through the single point representing the larvae of both groups (TL = 3, length = 1 cm, i.e., log length = 0) (Fig. 1). This leads to equations of the form

$$(4) \qquad TL = 3 + b \log_{10}(L)$$

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where the slope b expresses the change of TL with (log) body size, itself expressed in centimetres. This relationship generated relatively small differences of within-species mean TL when applied to observed length–frequency distributions of cod landings (Fig. 2). Nevertheless, we developed and tested two generic approaches — length and age based, respectively — for quantifying the effect on mean TL of changes in the size composition of exploited populations as a result of increasing fishing mortality.

Length-based relationship between fishing mortality and TL

Beverton and Holt (1956) showed that total mortality (Z) in fish populations whose individuals grow according to the von Bertalanffy growth function (VBGF) can be expressed by

$$(5) \qquad Z = [K(L_\infty - \bar{L})] / (\bar{L} - L_c)$$

where L_∞ is the asymptotic length, i.e., the mean size that the individuals in the population would reach if they were to live and grow indefinitely, K is the rate at which L_∞ is approached, and $\bar{L}$ is the mean length in the population computed from L_c upward. Here, L_c represents the length at entry into the fishery, assuming knife-edge selection. Using Z equals the sum of fishing (F) and natural (M) mortality, exploitation rate (E) defined as $E = F/Z$, M/K as the ratio of natural mortality to growth (with values usually between 1 and 3), and $E = 1 - (M/K)/(Z/K)$, we can rearrange eq. 5 to determine $\bar{L}$ as

$$(6) \qquad \bar{L} = [L_\infty + ([(M/K) / (1 - E)]\ L_c)] / ([(M/K) / (1 - E)] + 1)$$

for $0 \le E < 1$. Based on eq. 4, the change in TL (ΔTL) in a fish population where mean body sizes have been reduced by fishing can be estimated from

$$(7) \qquad \Delta\mathrm{TL} = b \log_{10} \left[\frac{L_\infty + \left(\left(\frac{M/K}{1-E} L_c \right) \Big/ \left(\frac{M/K}{1-E} + 1 \right) \right)}{L_\infty + (((M/K)\ L_c)/((M/K) + 1))} \right]$$

in which all parameters are as defined previously. The estimates of ΔTL thus obtained are approximate because the TL values corresponding to a mean length obtained from eq. 7 may differ from the mean TL value of an age-structured population, our next topic.

Age-based relationship between fishing mortality and TL

An explicit model for estimating the mean TL of an age-structured population in which TL changes linearly with (log) length is

$$(8) \qquad \mathrm{TL} = \frac{\left(\int_{t_r}^{t_c} N1_t A \mathrm{d}t + \int_{t_c}^{t_{max}} N2_t N3_t A \mathrm{d}t \right)}{\left(\int_{t_r}^{t_c} N1_t \mathrm{d}t + \int_{t_c}^{t_{max}} N2_t N3_t \mathrm{d}t \right)}$$

where $N1_t = e^{-M(t-t_r)}$, $N2_t = e^{-M(t-t_c)}$, $N3_t = e^{-F+M(t-t_c)}$, $A = 3 + b \times \log_{10} L_t$ (eq. 4), $L_t = L_\infty(1 - e^{-K(t-t_0)})$, i.e., the VBGF for growth in length with parameters L_∞ and K as defined above and t_0 setting the origin of the VBGF, t_r is the recruitment age, i.e., the age from which eq. 8 applies, t_c is the age at entry into the exploited stock, assuming knife-edge selection (i.e., corresponding to L_c), and t_{max} is the maximum age in the population.

Fishing mortality trends

We did not find data from which precise values of fishing mortality could be estimated for all the stocks included in the fisheries statistics described above. However, a time series of F, sufficient for estimating the potential effect of fishing on size compositions and hence on TL, is available for cod for the entire period covered here (Myers et al. 1995). Estimates of F for other east coast species, although for shorter periods, are also available in the database assembled by Myers et al. (1995), of which an updated version is included in FishBase (Froese and Pauly 1998). We obtained mean values of F by year for each species with suitable data by calculating average F weighted by the landing of each population of that species. These were subsequently grouped into a single estimate for "miscellaneous demersal fishes."

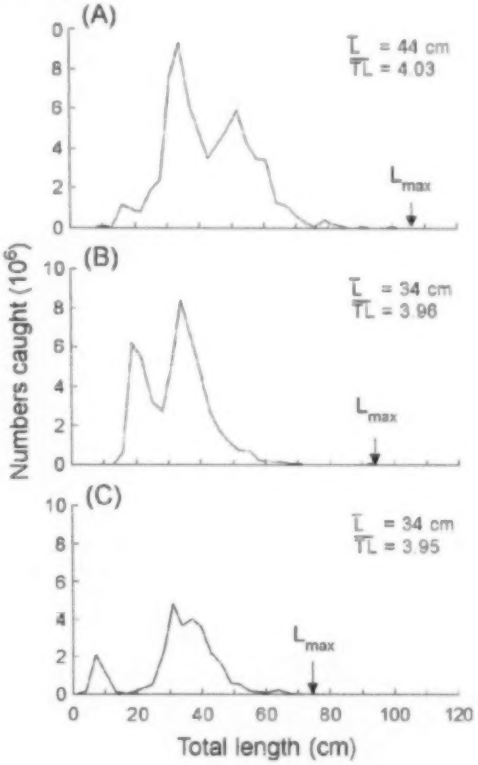

Fig. 2. Effects of changing size distributions on estimation of mean TL in Nova Scotian cod in (A) 1971, (B) 1992, and (C) 1999 based on the TL–size relationship for higher-order carnivores in Fig. 1. Note that mean TL changed by ~2% from 1971 to 1999 compared with ~25% for mean length and maximum size (L_{max}).

Results

The basic features of fisheries landings in the three areas considered here are illustrated in Fig. 3. For the east coast (Fig. 3A), overall catch trends were driven by cod landings until the mid- to late 1980s. On the west coast (Fig. 3B), overall catches are highly variable, due to the opening of successive "new" fisheries (marine mammals, Pacific herring (*Clupea pallasi*), Pacific hake (*Merluccius productus*)). In contrast, the landing statistics for inland waters (Fig. 3C) do not suggest any long-term trend.

We summarized the TL estimates from FAO statistics for these three areas in the form of catch pyramids to contrast the landings per TL class at the beginning (1950) and end

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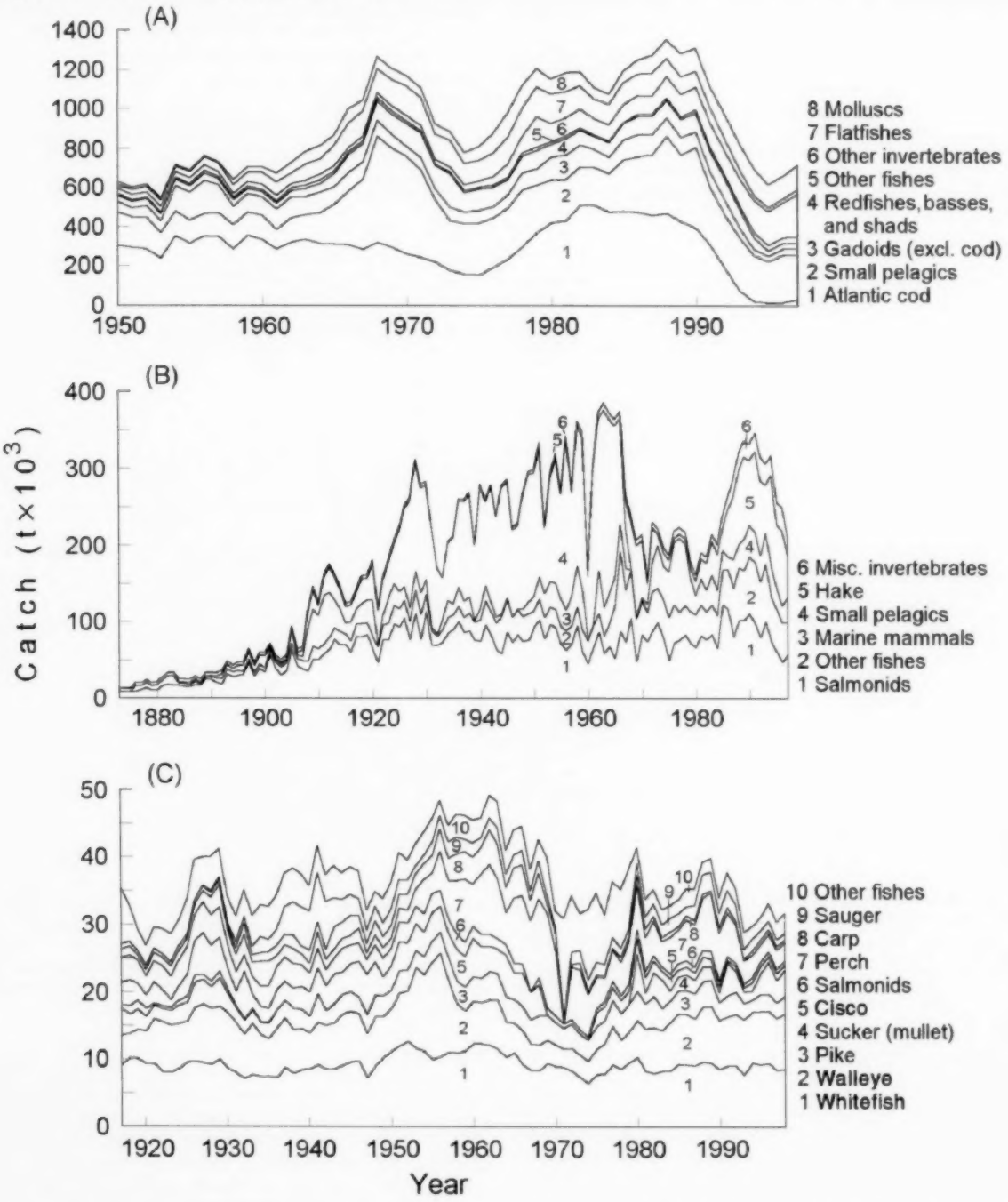
Fig. 3. Time series of aggregated fisheries landings from Canadian aquatic ecosystems (see text for sources): (A) east coast, 1950–1996; (B) west coast, 1873–1996; (C) inland waters, 1917–1997.



(1997) of the time series. The differences are very large for the east coast (Fig. 4A). The contribution of higher TL fish (especially cod) to the landings has decreased greatly, while that of invertebrates, of which the snow crab (*Chionoecetes opilio*) is now the most important, has greatly increased. For the west coast (Fig. 4B), the pyramid reflects the important contribution of Pacific herring to the 1950 landings. For inland waters (Fig. 4C), the pyramid represents a small decline in mean TL, from 3.62 in 1950 to 3.45 in 1997, without major shifts in the composition of the landings. However, the

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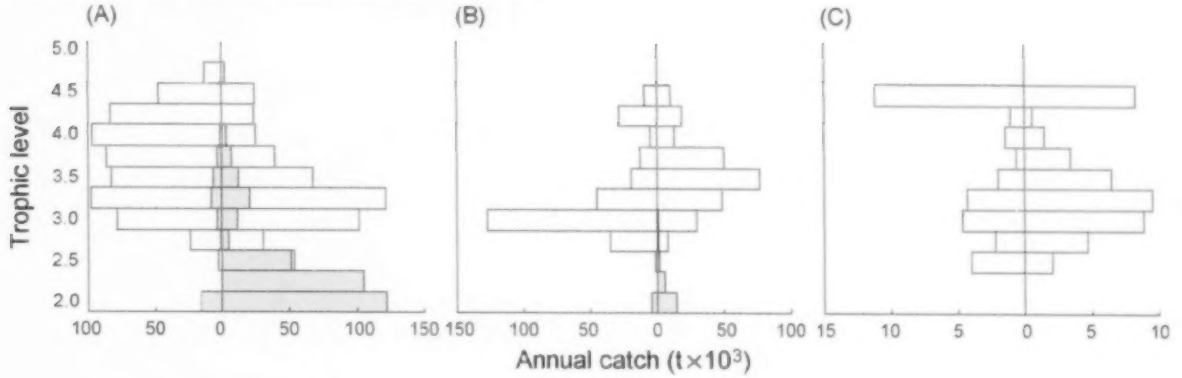
Fig. 4. "Catch pyramids" representing fisheries landings (open histograms, finfishes; shaded histograms, invertebrates) as a function of their TL (A) on the east coast, (B) on the west coast, and (C) in inland waters. Based on FAO statistics for 1950 (left side of the pyramid) and 1997 (right side) and TL estimates documented in FishBase (which includes a routine for automatic construction of such pyramids for any area with FAO data; Froese and Pauly 1998).



apparent decline is not borne out when longer time series data are used (Fig. 5C).

Trends in the mean TL of organisms in fishery landings for the three areas are illustrated in Fig. 5. There was a marked decline in the east coast fisheries from mean TL = 3.6–3.7 in the early 1950s to TL = 2.8–2.9 in the mid-1990s, or about 0.1·decade^{-1} (Fig. 5A). This decline persists if the analysis is made excluding cod, although the rate of mean TL decline is then halved, to about 0.05·decade^{-1}.

The trends for the west coast (Fig. 5B) are more complex. The simplest set of piecewise polynomials that fits the data (overall R = 0.50) suggests two periods with different TL trends: a linear increase in mean TL from 1873 to 1894, with a slope of 0.215 TL·decade^{-1}, followed by a period with fluctuating mean TL values and an overall negative TL trend of –0.032·decade^{-1} (Fig. 5B, inset). Exclusion of Pacific herring leads to a more moderate rate of decline, while exclusion of Pacific hake leads to a steeper rate of decline.

For inland waters, only the FAO data show a downward trend in mean TL (Fig. 5C). The more detailed and longer series of Canadian statistics documented in Table 3 do not confirm the existence of this trend (Fig. 5C). This difference is due, to a large extent, to our criterion of excluding marine fishes taken in estuarine waters. For example, the inclusion of rainbow smelt, which have a low TL (2.5) and relatively high landings (about 10^4 t·year^{-1} since the mid-1960s), would have led to a decrease similar to that observed for the FAO data.

Application of our length-based (eq. 7) and age-based model (eq. 8) produced roughly similar results (Fig. 6). Both models predict relatively small decreases in mean TL, except at the very high exploitation rates. However, the models predict that TL will decrease rapidly with increasing E when length at first capture is very small relative to asymptotic length, meaning that the fish are exposed to fishing throughout most of their lives.

Figure 7 documents key aspects of application of our age-based model to the east coast data. Figure 7A shows the available time series of fishing mortality for cod and miscellaneous demersal fishes. Figure 7B illustrates the change in the mean TL of cod given the F values in Fig. 7A, while Fig. 7C contrasts two series of mean TL for east coast catches, one uncorrected and the other corrected for the within-species effect of F-related body size changes on TL.

Discussion

Mean TL trends in inland waters

We start our discussion with freshwater ecosystems, as they tend to be small, at least relative to the range of most fishing craft. Human impact on these systems has therefore tended to occur earlier than accounted for by data such as assembled here. For instance, Smith (1995) noted that "Lake Ontario may have had the highest fishery yields of any of the other deepwater Great Lakes, but this occurred before the mid-1800s — before landings began to be recorded. The Atlantic salmon (*Salmo salar*) was the most-valuable species in the early fishery and was severely depleted before a quantitative account of the fishery could be made."

Thus, the stability suggested by our data for the inland waters of Canada does not preclude earlier anthropogenic changes that may have occurred in these ecosystems. Indeed, human interference, in the form of widespread introductions, has substantially altered the trophic structure of the Great lakes, as reflected, for example, in the relative abundance of coregonines (Fleischer 1992). Also, Pacific salmon, notably chinook (*Oncorhynchus tshawytscha*) and coho (*Oncorhynchus kisutch*), were introduced into the Great Lakes in several efforts ranging from hundreds to millions of individuals from the latter part of the nineteenth century up to the end of the twentieth century (Mills et al. 1993). These repeated introductions have resulted in self-reproducing populations that are generally too small to sustain anglers' catches. Hence, there has been the need for continuous restocking through hatchery programs, which, in the case of coho, are responsible for more than 90% of the total number of adult fish (Crawford 1997).

Our first conclusion, therefore, is that if time series of the mean TL of landed fish are to be useful for analyzing the impact of fisheries, the series must extend far enough into the past to cover major changes in the relative biomass of important ecosystem components. Also, such series must not

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Fig. 5. Time series of mean TLs (weighted by landings) from Canadian aquatic ecosystems: (A) east coast, 1950–1997, with (solid circles) and without cod (open circles); (B) west coast, 1873–1996, with (solid circles) and without Pacific herring (open circles) or Pacific hake (open squares); insert shows fitted piecewise polynomial model and 95% confidence intervals; (C) inland waters, 1917–1997, with Canadian (solid circles) and FAO statistics (open circles).

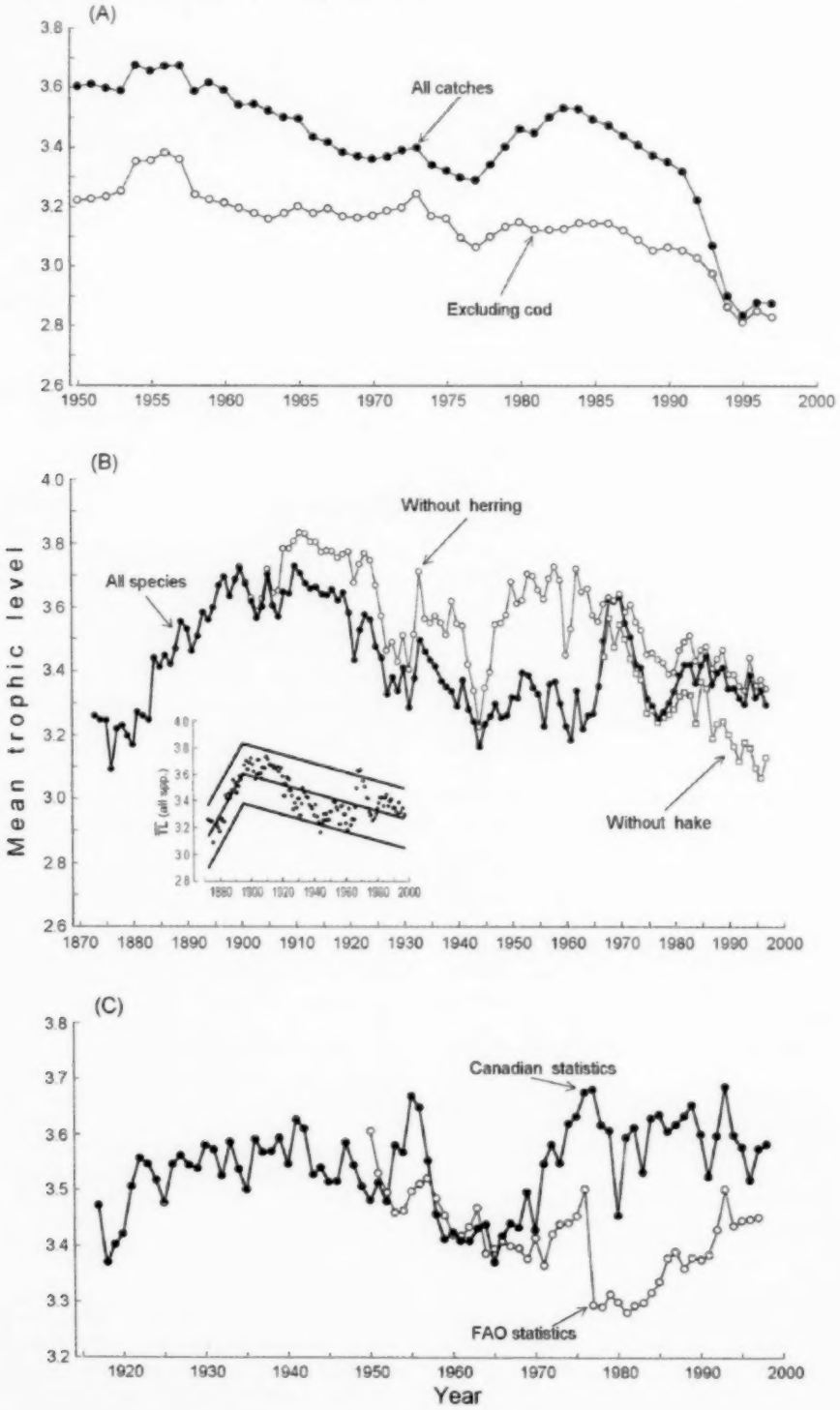

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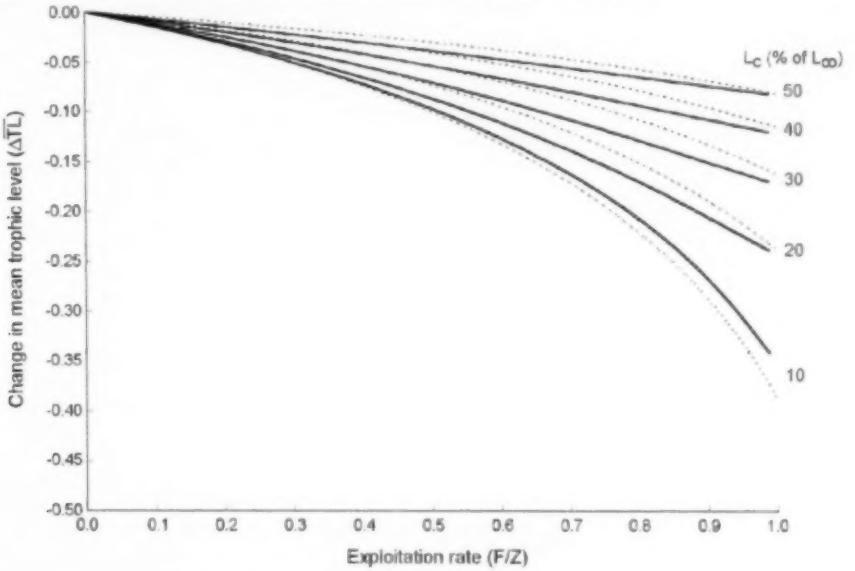
Fig. 6. Nomogram for estimating the effect of fishing (i.e., of $E = F/Z$) on the mean TL of a fish population with $M/K = 2$ for different values of the ratio L_c/L_∞ (see eq. 6 for definitions of E and M/K). Note that the length-based analysis (broken lines, from eq. 7) provides results roughly similar to those of the age-structured model (solid lines, from eq. 8).



be "contaminated" by anthropogenic impact other than withdrawals by fishing. In the case of Canadian inland waters, the confounding factor is stocking, which maintains relatively high biomass and catches of fishes with high TL (e.g., of Pacific salmon in the Great Lakes), counteracts any "fishing-down" effect, and thus precludes evaluation of sustainability based on mean TL.

Mean TL trends on the east coast

On the east coast, the operations until the 1970s of distant water fleets and the later deployment of a Canadian trawler fleet had a strongly negative impact on the mean TL of organisms in the landings. The decline in mean TL, while strongly influenced by fluctuations in the cod stock, was shown to occur also when this species is not included in the analysis.

Our new length- and age-based models produced roughly similar estimates of the effect of F on within-species mean TL. The differences between the results from the two models are accounted for by the fact that the length-based model predicts mean TL changes from a single mean length, while the age-based model estimates mean TL as integral of an age-structured population.

The application of the more accurate age-based model to cod and other demersal fishes showed that the within-species effect of size, and hence reduction in TL by fishing, is relatively small, at least when compared with the changes in mean TL due to the fluctuation of a single, abundant species (or its exclusion from the analysis, as shown for cod in the east coast and Pacific herring and Pacific hake in the west coast). This is especially true if the within-species effect involves taxa whose TL does not strongly increase with body size, as is the case for small pelagics (see Fig. 1) and probably for most invertebrates as well.

Overall, given their trend in mean TL, we conclude that the east coast fisheries are unsustainable at the ecosystem level.

Mean TL trends on the west coast

For the west coast, our results confirm Glavin (1996) who noted that overall landings tend to depend on the status of the latest "new" species. Presently, this new species is Pacific hake, and the development of a fishery for this high-TL predator is the reason why the mean TL of organisms in the fisheries is at its present height. Still, in spite of fluctuations caused by this and previous new fisheries (notably that for Pacific herring), the dominant trend in the twentieth century has been one of significant TL decline (-0.032·decade^{-1}). The preceding period of increasing TL (0.215·decade^{-1}), from 1873 to 1894, was largely due to the industrialization of the fisheries (formerly dominated by landings of low TL invertebrates), which enabled the catching of previously underexploited, large, high-TL predators (Pacific halibut (*Hippoglossus stenolepis*), marine mammals, etc.).

The catch pyramid for the west coast confirms the importance of long time series: the comparison of 1950 and 1997 (the period covered in FAO statistics) would suggest that the mean TL of organisms in the west coast fisheries has increased over time. The increase was due to the collapse of fisheries for small pelagics (predominantly Pacific herring), which have low TL, in the 1960s. Given our long time series of mean TL values and their overall trend, we conclude that the west coast fisheries are also unsustainable at the ecosystem level.

General features and uses of mean TL series

The time series of catches from the marine fisheries off the east and west coasts of Canada have covered sufficiently

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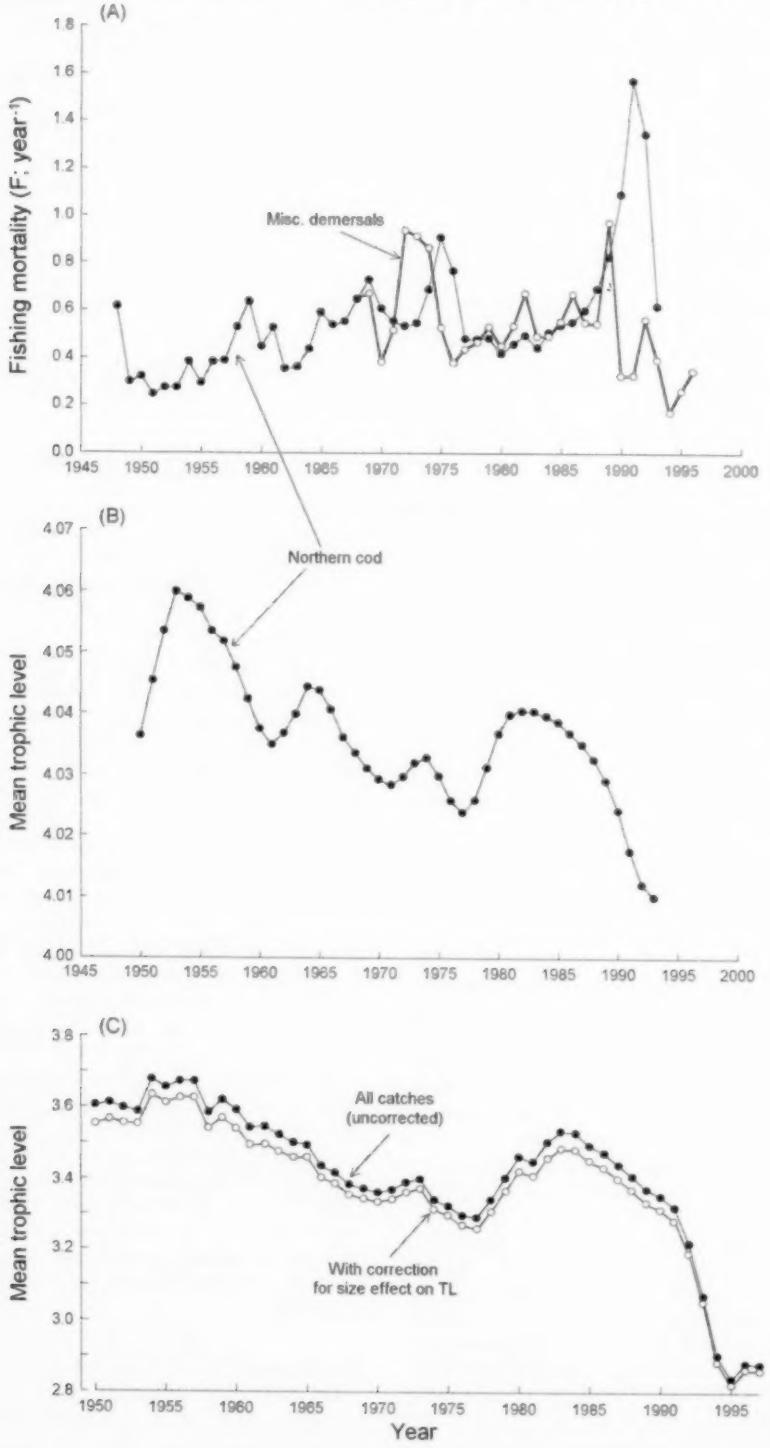
Fig. 7. Relationships between F and mean TL of organisms in Canadian east coast fisheries landings: (A) landings-weighted mean fishing mortality of demersal fishes (thick line, open circles) and of cod (thin line, solid circles) estimated for each year k from $F_k' = F_{k-4} + 2F_{k-3} + 3F_{k-2} + 2F_{k-1} + F_k/9$ to simulate equilibrium; (B) changes in mean TL of cod predicted by eq. 8, given the F_k' values in Fig. 7A and the parameters in Table 1, footnote *f*; (C) original (from Fig. 5A) and corrected time series of mean TL, i.e., considering the effects of cod size reduction, a similar effect on other demersal fishes, and no effect for pelagic fishes and invertebrates.



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long periods for significant downward trends in the mean TL of the fisheries to appear, thus providing local confirmation of the global trend toward "fishing down marine food webs" documented in Pauly et al. (1998). As pointed out, the time series for inland waters was not adequate for this purpose.

However, it is probably too early to make definite recommendations on how mean TL changes of organisms in landings from a given area could be used to generate precise reference points for ecosystem-based management. Deriving and evaluating potential indices is presently a very active area of fishery and ecosystem research, with consensus on suitable candidates well beyond the horizon. Nevertheless, the present study and the previous analyses by Pauly et al. (1998) allow the identification of diagnostic features that may be considered when such recommendations are made.

(1) An increasing trend in mean TL with increasing or stable total catches may have a number of causes, of which a frequent one is the development of new fisheries for previously unexploited high-TL groups such as offshore and (or) deep-sea species.
(2) Stable mean TL associated with stable total catches suggests sustainability.
(3) a continuous downward trend in mean TL combined with stagnating catches implies absence of sustainability. A continuous downward trend also implies a change in the species mix that is caught, including a transition toward low-TL invertebrates as mean TL drops below 3, the lower limit for non-herbivorous fishes, documenting a fishery now relying strongly on invertebrates.
(4) A decline in mean TL combined with declining catches (including discards) in the absence of change in fished area or gear deployment may imply a food web collapse (possibly the reason for the accelerated mean TL decline in east coast noncod species in the early 1990s), with biological production diverted toward presently unexploited components of the ecosystem such as small benthic invertebrates and (or) jellyfish.

One way to use series of mean TL of organisms in fisheries catches that would combine these four diagnostics and allow drawing inferences on sustainability would be to plot the annual mean TL of "traditional" species (i.e., excluding catches of species not previously exploited) against the corresponding catches (including discards). Given the "pyramidal" nature of marine ecosystems, such plots should exhibit, given sustainability, a straight descending slope reflecting the relationship between biological production and mean TL, i.e., transfer efficiency (Pauly and Christensen 1995). On the other hand, lack of sustainability would lead to departures from linearity and in extreme situations (diagnostic 4) to the "backward-bending" curves of TL versus catch observed by Pauly et al. (1998).

Further, comparisons among mean TL series from similar ecosystems (e.g., around the North Atlantic or the North Pacific) may allow detection of similarities among the mean TL values at which plots of TL versus catches start to bend backward. This in turn may lead to the identification of a generic cutoff point for mean TL, at least for the ecosystem type in question. Obviously, such analyses would have to be conducted repeatedly, with different species groups excluded in order to obtain results unaffected by minor fluctuations in the biomass and catches of individual species.

In any case, the time series used in such analyses should be as long and accurate as possible, lest they induce grossly erroneous interpretations. It was surprising that there was no consistent series of official Canadian catch data. Also, the landing series that may be constructed from official documents and statistics do not match the FAO series based on data supplied to the FAO by the Government of Canada, an FAO member state. Therefore, we cannot but wonder how the detailed assessments of various single-species fisheries routinely conducted in Canada can avoid being marred by the shifting baselines (Pauly 1995) that result from lack of consistent time series that reach well into the past.

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Prediction and the aquatic sciences[1]

Michael L. Pace

Abstract: The need for prediction is now widely recognized and frequently articulated as an objective of research programs in aquatic science. This recognition is partly the legacy of earlier advocacy by the school of empirical limnologists. This school, however, presented prediction narrowly and failed to account for the diversity of predictive approaches as well to set prediction within the proper scientific context. Examples from time series analysis and probabilistic models oriented toward management provide an expanded view of approaches and prospects for prediction. The context and rationale for prediction is enhanced understanding. Thus, prediction is correctly viewed as an aid to building scientific knowledge with better understanding leading to improved predictions. Experience, however, suggests that the most effective predictive models represent condensed models of key features in aquatic systems. Prediction remains important for the future of aquatic sciences. Predictions are required in the assessment of environmental concerns and for testing scientific fundamentals. Technology is driving enormous advances in the ability to study aquatic systems. If these advances are not accompanied by improvements in predictive capability, aquatic research will have failed in delivering on promised objectives. This situation should spark discomfort in aquatic scientists and foster creative approaches toward prediction.

Résumé : La nécessité de la prédiction est maintenant largement reconnue, et souvent formulée comme un objectif des programmes de recherche en sciences aquatiques. Il s'agit là en partie de l'héritage d'une position préconisée par l'école de la limnologie empirique. Cette école présentait toutefois la prédiction de façon étroite, et ne parvenait pas à rendre compte de la diversité des approches prédictives ni à placer la prédiction dans un contexte scientifique adéquat. Des exemples tirés de l'analyse des séries chronologiques et de modèles probabilistes orientés vers la gestion permettent d'élargir les approches et les perspectives de la prédiction. Le contexte et la justification de la prédiction est une amélioration de la compréhension. Il est donc nécessaire de voir la prédiction comme une aide à la construction du savoir scientifique, une meilleure compréhension amenant à une meilleure prédiction. L'expérience montre toutefois que les modèles prédictifs les plus efficaces consistent en une représentation condensée des caractéristiques clés des systèmes aquatiques. La prédiction reste importante pour l'avenir des sciences aquatiques. Les prédictions sont nécessaires pour évaluer les problèmes environnementaux et pour tester les bases scientifiques. La technologie permet des progrès remarquables dans les moyens d'étude des systèmes aquatiques. Si ces progrès ne s'accompagnent pas d'une amélioration de la capacité de prédiction, la recherche en sciences aquatiques n'aura pas réussi à atteindre les objectifs promis. Cette situation, qui semble dérangeante pour les chercheurs en sciences aquatiques, doit susciter la recherche d'approches créatives de la prédiction.

[Traduit par la Rédaction]

Introduction

In the final year of his life, the Canadian limnologist F.H. Rigler published two papers promoting an "empirical approach" to the development of general theories in the aquatic sciences. One paper argued that many phenomena studied by ecologists were unpredictable, at least based on current theory (Rigler 1982*a*). As an alternative to focusing on phenomena that were conceptually obscure or inherently unpredictable, Rigler advocated seeking general relationships such as regression models to identify ecological properties and processes that were predictable. By starting from empirical relationships, more "explanatory theories" would likely emerge, providing a better basis for scientific advancement. A second paper called for a closer integration of fisheries science and limnology (Rigler 1982*b*). Rigler complained that traditional limnology and fisheries science were far too separate given many common problems. He again promoted predictive approaches within and among the two disciplines as means toward achieving integration. These two papers presented an outline of an approach that become widely known as "empirical limnology" and was a strongly advocated by both Rigler and R.H. Peters in numerous papers and books (e.g., Rigler 1975; Peters 1991; Rigler and Peters 1995).

While the philosophy of the empirical limnologists was highly controversial (Lehman 1986; Carpenter and Kitchell 1988; Shrader-Frechette and McCoy 1993), the work of Rigler, Peters, and associates focused attention on the issue of prediction. The significance of prediction either as a component of the scientific process or as a means toward improved application of the aquatic sciences was either not widely appreciated or at least not widely discussed prior to their work. This has changed. In this essay, I contend that there is now an increased recognition of and emphasis on prediction in the aquatic sciences. The need for predictions

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is clear. The public that funds most aquatic research does so partly in the hope that science will facilitate better management and protection of precious resources. Better management would follow from a more predictive science that could forecast the consequences, costs, and benefits of management actions. For purely disciplinary reasons, there is also a need for predictions to hone, test, and organize theoretical ideas. Thus, it is appropriate to reflect on the concept of prediction in this volume that attempts to foreshadow future concerns and directions for the discipline.

It is important to note at the outset that the ensuing discussion of prediction in this paper is not meant to be placed in opposition to the goal of understanding in science. While some empirical limnologists in the past minimized understanding as a scientific objective (e.g., Peters 1991), the discussion here is oriented toward integrating prediction and understanding.

One reason for discussing the interaction of prediction and understanding is that past examples of predictive approaches, especially those deriving from the empirical limnologists, largely represent only one of many possible approaches to prediction. As a consequence, there is a danger that prediction has been viewed too narrowly or, worse, as inapplicable to many scientific endeavors. I argue that there are a variety of approaches to making predictions and a need for an expanded view. Predictive approaches can and should interact productively with mechanistic studies and experiments. By reconciling these different facets of scientific activity, prediction takes a significant but not dominant place within research programs designed to enhance scientific understanding and contribute to the improved management of aquatic systems.

Prediction defined

Prediction in common usage is foretelling or stating in advance an outcome based on some belief or experience. In science, predictions derive from theory. In keeping with the common definition, theory represents scientific experience from which predictions are derived, but this analogy has limits. Theories are organized bodies of knowledge that consist of a set of conceptual constructs that offer causal explanations of some domain of observable phenomena (Pickett et al. 1994). Thus, predictions drawn from scientific theory are to be taken differently from those provided by clairvoyants. Theories represent a very special form of experience. They are the organization of scientific knowledge.

The logical structure of a theory allows mathematical, graphical, and verbal descriptions of natural phenomena. These descriptions lead to predictions that, given a set of circumstances or precedents, a particular result or response should be observed. Some distinguish between predictions and forecasts (Pickett et al. 1994). The latter do not necessarily derive from theory and may be largely correlative, reflecting little understanding but nonetheless still useful in science. The most common use of forecasting is to project current knowledge into the future using a model. Thus, forecasting is based on or includes time. Predictions can be time independent. For example, a theory might suggest an evolutionary pattern or process that could then be tested by gathering data from fossils or by an experiment.

Despite these distinctions between prediction and forecasting, I will lump the two in this paper. Many scientific predictions seem hybrids of those extracted specifically from theory with those derived more loosely from various types of models that may not have the status of theory. Recognizing the difference in practice is difficult, and there are surely differences among scientists about what body of knowledge constitutes theory (and hence provides predictions) and what body of knowledge is less well established theoretically and hence does not yield formal predictions. Much of the knowledge in aquatic science is organized loosely, if at all, into theory. The goal for most practicing scientists is to predict usually with some form of a model, and so I focus on predictions in this sense.

An important recognition is that predictions in the aquatic sciences are usually probabilistic. We seek models that define the most likely state or states of nature and their uncertainties. This is particularly the case when making predictions for management (Walters 1986). Various means for making such predictions are available including Bayesian and maximum likelihood approaches (Hilborn and Mangel 1997). The key point is that predictions derive from models of the natural world that express or amalgamate scientific understanding of a problem. Probabilities in predictions represent an important feature in expressing the quality of scientific knowledge, as a means of communicating to nonscientists, and as a source of inspiration for scientific research that seeks to reduce uncertainty.

Prediction as a goal

Large-scale global environmental problems have spawned many national and international research initiatives and targeted programs in all areas of environmental science. These efforts usually have mission statements that reveal prediction as a core objective.

Mission statements from two marine programs are representative. The U.S. Global Ocean Ecosystem Study (GLOBEC) seeks to "develop basic information about the mechanisms that determine the variability of marine animal populations" (www.nsf.gov/geo/egch/gc_globec.html). Studies that couple physical and biological processes are proposed to achieve this objective. The goal for prediction in this case comes second: "Once projects directed toward understanding the impact of physical phenomena in marine ecosystems are well advanced, U.S. GLOBEC investigators must address the question of predicting the future responses to the climatic scenarios that researchers deem probable in the sea." The international version of this program has a similar goal with a component specifically focused on Atlantic cod (*Gadus morhua*) (www.pml.ac.uk/globec/):

> The International Council for the Exploration of the Sea (ICES) and GLOBEC have joined together to develop an innovative programme to advance the **understanding and prediction of variability in fish** stock recruitment, both in the short term (annual forecasts) and in the long term ("climate effects"). Cod has been chosen to serve as the candidate species for this exercise because its biology is well-known and supported by ample data bases, it has a

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> pan-Atlantic distribution, and its abundance and distribution have been shown to be sensitive to specific past examples of environmental variability. These considerations provide Cod and Climate Change (CCC) with the possibility of developing new capabilities in predicting fish recruitment from a better understanding of the interaction of physical processes and population dynamics.

This quote illustrates that large programs like GLOBEC not only have general scientific goals, but also specific ones that are of immense practical importance.

Similar to GLOBEC, the U.S. portion of the international Joint Global Ocean Flux Study (JGOFS) has two core objectives (www1.whoi.edu/mzweb/overview.htm). The first is "to determine and understand on a global scale the processes controlling the time-varying fluxes of carbon and associated biogenic elements in the ocean, and to evaluate the related exchanges with the atmosphere, sea floor, and continental boundaries." The second is "to develop a capability to predict on a global scale the response of oceanic biogeochemical processes to anthropogenic perturbations, in particular those related to climate change." The JGOFS and GLOBEC examples are justified partly in the context of anticipated global climate change and partly in the context of the need to view the ocean system at very large scales including the global scale. The consequences of climate change are the major goals for prediction in these studies.

Limnologists are also interested in prediction. One example is the Freshwater Imperative, a general research agenda designed to "identify research frontiers and opportunities in limnology" (Naiman et al. 1994). The goal of the Freshwater Imperative is "to acquire a *predictive* understanding of freshwater ecosystems and resources that can be used to improve detection, assessment, and forecasting of environmental effects and to develop management and mitigation alternatives for scenarios of potential environmental change." Much like the marine programs, prediction is viewed here as first being fostered by basic scientific understanding and second serving as a means to develop better management of freshwaters in the context of a changing environment. Prediction is in this case and for the GLOBEC cod study cited above a way of connecting research programs to pragmatic endpoints.

A cynic might argue that these mission statements of large programs are designed primarily to persuade the funders of science to support basic research with prediction and application as props to make the research efforts appealing. While I agree that their purpose is to promote research, I believe that these statements also reflect the growing aspirations of many scientists to use their work in addressing demanding environmental problems. My view is supported by calls from both scientific societies and distinguished researchers for work directed at the problems of human-driven environmental change (e.g., Lubchenco et al. 1991; Vitousek 1994; Tilman 1998).

The mission statements of large research programs are also evidence that the need for prediction identified by the early empirical limnologists has in fact diffused widely through the aquatic sciences. The challenge, of course, is to deliver on these statements and actually provide predictions. One way the cynical and the aspiring should judge large research programs retrospectively is to determine not only how the programs contributed to scientific advances, but also the quality of predictions that were actually produced.

Types of prediction

The empirical limnology school presented prediction in the form of regression models (Peters 1986, 1991). The approach was largely based on comparisons among aquatic systems. This gave the resulting models generality and established patterns against which to evaluate other systems.

While these models are useful and their predictions easily understood, the approach has shortcomings. First, regressions as used in this context predict only the annual or seasonal means for a given system based on data from multiple systems, and the resulting predictions are usually imprecise. An example is a study that I conducted of zooplankton biomass (Pace 1986). A regression model summarized the relationship between mean summer zooplankton biomass and lake total phosphorus (TP) explaining 86% of the variation. Confidence limits, however, were wide, and the model provides a poor basis for predicting the biomass of zooplankton in an individual lake. For example, assuming a typical lake in the data set with a TP of 12 $mg \cdot m^{-3}$, predicted mean zooplankton biomass within the 95% confidence interval varies roughly threefold. Such models are not very useful, either for drawing inference in specific cases, for modeling, or for managing individual systems. These shortcomings and criticisms of regression predictions from comparative studies have been previously noted (Shapiro 1979; Carpenter and Kitchell 1988; Carpenter et al. 1991) as have statistical problems associated with regression methodology (McArdle 1987; Prairie et al. 1995).

Nevertheless, the shortcomings of regressions are not a reason to dismiss the empirical approach. Comparative analyses provide a means of evaluating patterns. For example, in my study noted above, one question concerned whether residual variation in relationships between phosphorus and chlorophyll concentrations in lakes could be partly explained by zooplankton biomass or community size structure. Comparative analysis revealed that zooplankton biomass did not explain residual variation in phosphorus–chlorophyll relationships, but the relative dominance of larger zooplankton was associated with lower chlorophyll per unit TP (Pace 1984). The results of this study illustrate how comparative studies can be used to evaluate and test aspects of general patterns. The effects of grazers on primary production in aquatic systems have become a central research topic as evidenced by further comparative work (Carpenter et al. 1991; Quirós 1998) as well as experimental and theoretical studies (Carpenter and Kitchell 1993; Scheffer 1998).

Comparison of systems remains a valuable and now accepted means of evaluating and debating generalizations. Comparative papers are often well cited. For example, in the highly experimental field of aquatic microbial ecology, papers on methods, concepts, and comparisons were among the 10 most cited (Duarte et al. 1997). The contributions of comparative studies can also stimulate debate and raise new questions. Current discussions regarding the relative rates of primary production and respiration in the ocean are largely based on comparisons of data from many studies, the result-

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ing statistical models, and interpretations of both the data and models (Del Giorgio et al. 1997; Duarte and Agusti 1998; Williams 1998).

A limitation of comparative studies is that they usually focus on prediction of means at the scale of a system with little consideration of temporal dynamics or spatial variation. Yet these latter features are critical in structuring ecological systems and determining variation. Other types of predictions for other scales of resolution are often needed, and a variety of models suitable for making these predictions are available. This paper cannot consider all the possibilities or review the various statistical and simulation approaches to prediction. Some of the situations requiring different types of predictions can be noted, and these naturally suggest possible models and approaches. When considering aquatic systems, we can imagine that predictions are needed for the future state or dynamics of a system (temporal predictions), for a new place (spatial predictions), for a new circumstance (altered systems), as well as for general cases. These problems are typically approached both formally and informally with verbal and graphical models. These models do not provide estimates of uncertainty, and so, analytical, statistical, and simulation modeling methods are needed. Regression models are most suitable for some predictions in the last category (general case). Other statistical approaches such as time series analysis, geostatistics, and Bayesian methods are useful for predictions about time, place, and altered state (e.g., consequences of a management action), respectively. Analytical and simulation models can also serve as predictive tools and can be applied to many problems (e.g., space, time, altered state). Large-scale simulations are the tools envisioned by the global marine programs noted above (GLOBEC, JGOFS) for making predictions about the ocean under scenarios of changing climate. Sensitivity analysis and simulations of varying scenarios can be used to assess uncertainty with these models.

Examples of prediction

Some examples are useful to portray the application of predictive models to problems not suitable for standard linear regression. Dynamic interactions are a central feature of ecological systems. Dynamic models are useful to project present and future changes of ecological systems. There are several approaches to dynamic models, including mechanistically oriented simulations and statistically oriented methods of time series analysis. A time series model of rotifer dynamics illustrates the approach and the forecasts (predictions) that such models can make. Figure 1*a* presents rotifer abundance before and after the invasion of the zebra mussel (*Dreissena polymorpha*) in the Hudson River estuary, New York, U.S.A. (Pace et al. 1998). Zebra mussels invaded the Hudson in the early 1990s and became abundant in 1992. At that time, there was a precipitous drop in both phytoplankton and microzooplankton biomass that has subsequently been sustained (Strayer et al. 1999). A time series model based on data for 1986–1995 captures this shift by including a term for the presence or absence of zebra mussels (Fig. 1*a*).

The model can be tested by comparing forecasts with data from 1996 (Fig. 1*b*). Predictions from the model are well correlated with observations ($r = 0.81$, $p = 0.004$). The model, however, underrepresents the dynamics of the rotifer community, missing both maxima and minima in the time series (Fig. 1*b*), suggesting that additional parameters are needed and that measurement error along with natural population variability increases the overall variation in the data relative to that predicted by the model. Nevertheless, the model does represent the principal features of rotifer dynamics and further predicts a rapid recovery (not shown) were zebra mussels to decline.

The time series model is limited in that it contains no specific mechanism for the relationship between rotifer abundance and zebra mussels. Two possible mechanisms causing the decline were reduction in rotifer food and (or) direct consumption of rotifers by zebra mussels (Pace et al. 1998), but the model is purely empirical and does not distinguish among these likely causes or other less plausible mechanisms (e.g., an effect of zebra mussels on other species that in turn affect rotifer abundance or a disease introduced by zebra mussels that impacts rotifers). Experiments could distinguish among some of these mechanisms, and an alternative model could incorporate mechanisms but would require increased knowledge of the system and the estimation of additional parameters.

While not presented in Fig. 1*b*, the rotifer forecasts have associated confidence intervals. Predictions as probabilities are particularly useful in the context of management problems. In many aquatic systems, harmful algal blooms are a serious concern, and reductions in nutrient loading are often a proposed management action. How can the benefits of reductions or dangers of excess loading best be stated given the inherent uncertainties? Stow et al. (1997) illustrated an approach using a 19-year record of cyanobacterial blooms in Lake Mendota, Wisconsin, U.S.A. A logistic regression that includes observation error in the independent (spring TP) and dependent variables (mean summer biomass of cyanobacteria) provides a model for the data (Fig. 2*a*). This model can then be used to state specific probabilities of a high-biomass or bloom year for a given spring TP (Fig. 2*b*). For example, if loading is relatively low such that spring TP is 0.08 $mg \cdot L^{-1}$, the probability of mean summer cyanobacterial biomass exceeding a bloom threshold (5 $\mu L \cdot L^{-1}$) is only about 5%. If spring TP is 0.12 $mg \cdot L^{-1}$, the probability increases dramatically to greater than 60%. Hence, management efforts to lower spring TP to a threshold below 0.08 $mg \cdot L^{-1}$ would dramatically lower the risk of blooms.

A second example of probabilistic predictions is a decision table for a fishery modified from Hilborn et al. (1993). The average yield over a 5-year period is projected based on a stock–recruitment model. Three states of the population are considered along with the probability associated with each stock biomass for two harvesting scenarios (Table 1). The example makes it clear that the variable outcomes of management depend on both harvesting policy and the uncertain state of the population. Harvesting at a 200-kt quota in the first year and at 26% of the stock in subsequent years could result in either the highest or the lowest yield depending on the true biomass of the population (Table 1). While this example is somewhat simplified relative to an actual fish population management problem (Hilborn et al. 1993), the key point is that the various yields represent predictions of a series of alternative states. These predictions form a basis

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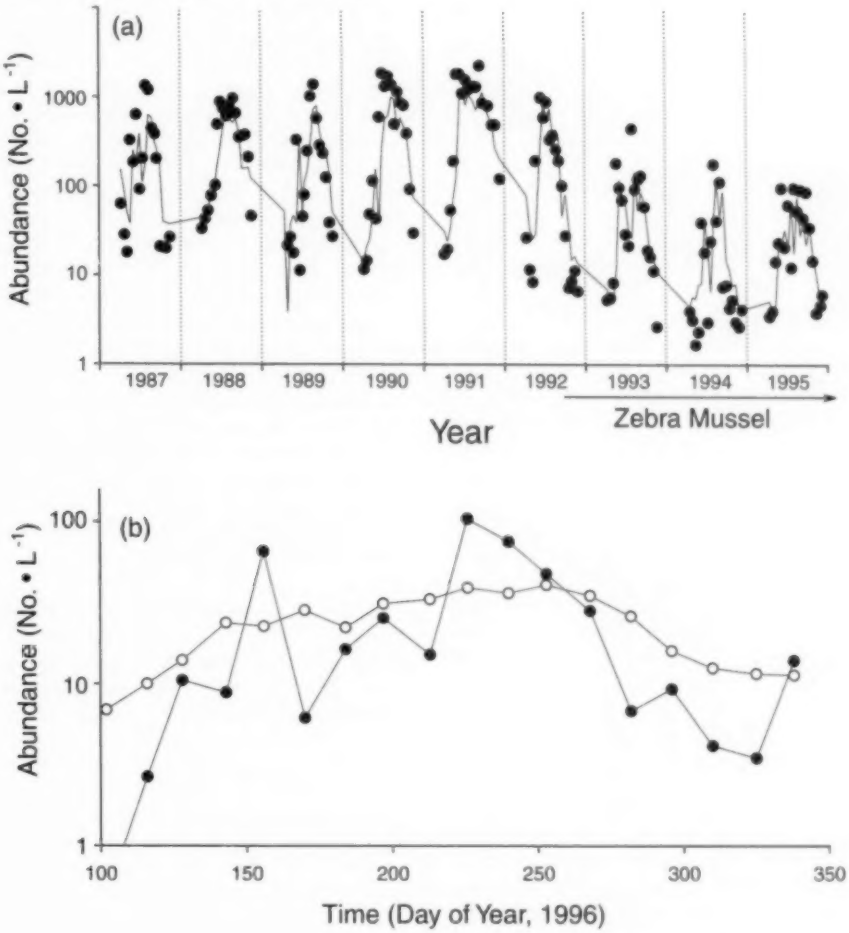
Fig. 1. (*a*) Time series model (line) and measurements (circles) of rotifer abundance in the Hudson River. Zebra mussels invaded the Hudson, resulting in a significant decline of rotifers beginning in 1992. (*b*) Forecasts from the model (open circles) are compared with data (solid circles) for the year 1996. The model and data for 1987–1995 are from Pace et al. (1998), with forecasts compared with previously unpublished data. Note the log scale on the ordinate.



for summarizing and presenting information to decision-makers, and they make explicit the uncertainties and risk.

The examples that I have presented are necessarily simple because of limited space to convey details. Thus, I have not specifically described either a simple general model (e.g., stock–recruitment, chemical mass balance) or a more complex simulation model (e.g., nutrient cycling, energy flow, population dynamics) because these are more difficult to explain. A variety of models of modest to more substantial complexity are useful for making predictions. Such models are used in forecasting to evaluate scenarios like climate change. This type of forecasting has been (e.g., De Stasio et al. 1996; Stefan et al. 1996) and will likely continue to be an important research topic. One goal should be to challenge predictions from these forecasts as much as possible with data in order to assess the quality of projections and to give credibility to the modeling. This comparison can be accomplished by evaluating models with data from paleo- and contemporary studies not used in the formulation of the original model. This form of prediction and comparison with data needs to become a standard by which models are presented and their contribution evaluated.

Table 1. Sample decision table showing the expected yield of a fishery over 5 years for three states of the stock and two harvest rates.

	Stock biomass (probability)		
Policy	0.9 Mt (0.57)	1.5 Mt (0.40)	2.1 Mt (0.03)
Constant 150-kt quota	136	150	150
200-kt quota (year 1)	122	154	166

Note: Probabilities for the stock biomass are indicated in parentheses. Quotas are constant for the first policy (150-kt quota) or at a percent harvest rate (26%) of the stock after a set quota in year 1. The example is modified from table 2 of Hilborn et al. (1993).

In the context of model–data interaction, biological oceanographers are adopting data assimilation methods from meteorology and physical oceanography (e.g., Lawson et al.

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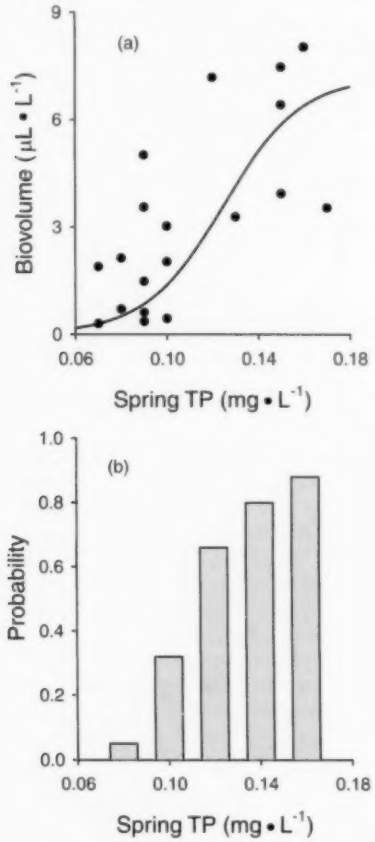
Fig. 2. (*a*) Relationship between spring TP and cyanobacterial biovolume in Lake Mendota, Wisconsin, based on annual means from 19 years of observations. (*b*) Probabilities for cyanobacteria exceeding a bloom threshold ($5\,\mu L \cdot L^{-1}$) as a function of spring TP based on the model presented in Fig. 2*a*. The model and data are from Stow et al. (1997).



1996; McGillicuddy et al. 1998; Spitz et al. 1998). Essentially, this approach involves updating forecasts derived from models. Data are iteratively "assimilated" into the model and used to improve the time-evolving simulation. This approach is especially germane to complex, dynamic situations where long-range forecasts are unlikely to be accurate. Weather forecasting that tracks the development and progression of storms provides a familiar example. Advances in data acquisition and processing make the use of assimilation methods feasible in some cases for coupled physical–biological models.

Data assimilation methods might be particularly useful for event-related forecasts of critical phenomena such as harmful algal blooms (Franks 1997). In this case, combinations of remote sensing of plant pigments in conjunction with hydrodynamic models and possibly in situ measurements (e.g., temperature, currents) would provide the basis for models to forecast the formation, evolution, and fate of blooms. This vision of forecasting might be applicable to many applied situations where variable ecological processes affect endpoints of human interest and management concern.

Interaction of prediction with mechanism and understanding

One criticism of predictive approaches is that predictions can be based on poor understanding and still yield statistically significant correlations. For example, a good prediction of the number of priests in North American cities could probably be obtained by counting the number of painters in phonebooks. Analyses of ecological systems suffer from this problem, as many of the independent variables are correlated (Downing 1991). Further, in highly interactive aquatic systems, so-called dependent variables may not be truly dependent but feed back on and affect the state of independent variables. These problems with prediction are, however, correctable when there is an appropriate interaction between scientific understanding and prediction.

All predictions are subject to refutation — this is a real strength. Hence, predictions based on poor principles such as my priest–painter example can be rooted out by appropriate testing and refinement. More importantly, prediction can and should interact profitably with mechanistic understanding. This interaction should improve prediction while keeping the mechanistic science aimed squarely at the problem. Coupling predictive goals with mechanistic studies helps to avoid narrow inquiry with little or no improvement in global understanding. Thus, prediction and understanding are interactive.

Better understanding can lead to better models facilitating better predictions, but this relationship is not absolute. We cannot define all the mechanisms of aquatic systems and hope to build models based on a complete understanding of all parts. Mechanistic research may not contribute to prediction, even though science is often pursued as if the only way to build valid predictions was through detailed studies (Walters 1998). Experience suggests instead that key mechanisms need to be collected into relatively condensed models. This is where prediction and understanding come together. Condensed models work because they capture critical processes that drive aquatic systems. The challenge remains to integrate understanding of specific mechanisms at various spatial and temporal scales in order to derive effective and reasonable models for relevant problems. This line of thinking raises questions concerning limits to prediction. Will successful predictions inevitably be mostly limited to short time and system-specific scales or can we achieve longer term and among-system predictions? At present, I do not think that this question can be answered. In the future, organizing and assessing predictive ability over various scales will likely be an important task.

An example of condensed models enhanced by understanding is illustrated by a study of metal concentrations in the common aquatic dipteran larvae *Chaoborus punctipennis* (Hare and Tessier 1996). In this study, concentrations of Cd were measured in water and in larvae for 23 lakes. Predictions of the concentration of Cd in larvae are poor when the free ion concentration of Cd (i.e., Cd^{2+}) is used (Fig. 3*a*). Predictions are improved when the competition between H^+ and Cd for biological uptake sites is taken into account (Fig. 3*b*). The prediction is further improved when the availability of Cd is calculated using models that estimate Cd complexation by dissolved organic matter (Fig. 3*c*). Thus,

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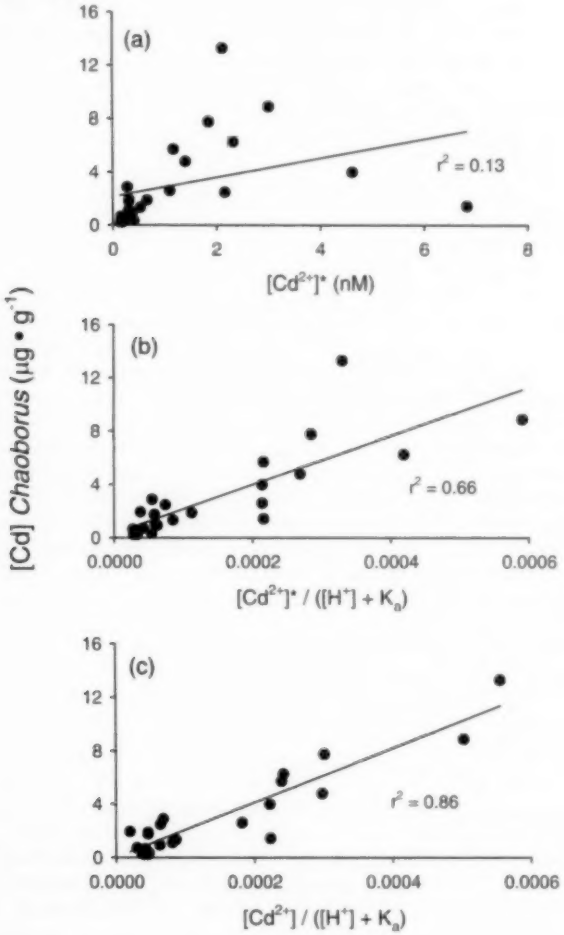
Fig. 3. Relationship of Cd concentrations in *Chaoborus punctipennis* to (*a*) free metal ion concentration, (*b*) free metal ion concentration normalized for competition between Cd and H^+ for biological uptake sites where K_a is the equilibrium constant of acid relative to uptake sites, (*c*) and as in Fig. 3*b* but where Cd concentration is also corrected for complexation with dissolved organic matter. Data and relationships are from Hare and Tessier (1996).



understanding the chemical interactions affecting the availability and uptake of Cd substantially improves predictions and leads to a relatively condensed model for that purpose (Hare and Tessier 1996). Predictions from this model have been extended and applied to other species of *Chaoborus* over a wide range of environmental conditions (Hare and Tessier 1998). The model works well because *Chaoborus* do not appear to regulate Cd, and hence body burdens reflect environmental conditions, and because the model derives from first principles of chemical activity and availability (Hare and Tessier 1998). This example illustrates the interaction of prediction and understanding. The goal of science is understanding, which is defined by Pickett et al. (1994) as "an objectively determined, empirical match between some set of confirmable, observable phenomena in the natural world and a conceptual construct." Prediction, therefore, is not an end but a means to better understanding.

While purely statistical models such as those promulgated by the empirical limnologists have a place in building scientific understanding, they are at best precursors for models derived from more fundamental principles. Livingstone and Imboden (1996) described this distinction well for models of lake hypolimnetic oxygen depletion. In their terms, "inductive models" are purely empirical, statistical fits between independent and dependent variables, while "deductive models" utilize general principles to make predictions for specific cases. The latter models fit the formal job ascribed for predictions derived from theory. In the case of lake oxygen models, inductive or empirical models employ sets of predictor variables to describe oxygen depletion. Deductive models utilize general functions of volumetric oxygen consumption (associated with the water) and areal oxygen consumption (associated with sediments) to describe oxygen depletion. These deductive models have the advantage of being easily understood and may provide better predictions where conditions are novel (e.g., climate change) (Livingstone and Imboden 1996).

Interestingly, it is typically the case that so-called "deductive models" are often based partly on purely empirical information, while "inductive models" are closely connected to general principles. For example, in the case of oxygen models, the volumetric rate of oxygen consumption in the deductive model of Livingstone and Imboden (1996) is a fixed value derived from widespread observations. This handy empiricism works well but begs the question why or if all lakes share a rather similar value of microbial oxygen consumption in the hypolimnion. The inductive models of the empirical limnologists are not derived simply from convenient correlations without conceptual content. The most enduring of these models such as those that describe lake eutrophication (Dillon and Rigler 1974; Vollenweider 1976) are based on two general concepts. The first is elemental mass balance and description of that balance by a continuously stirred reactor model. The second general concept is that nutrients may limit primary and secondary production in ecosystems. Both concepts are critical foundations for the success of the subsequent empirical descriptors known as nutrient loading models (Smith 1998).

Livingstone and Imboden (1996) were correct to call for the formulation of models in more fundamental terms wherever possible. This facilitates better application and more widespread possibilities for prediction. I view their distinction of inductive and deductive models as useful, but there is a need to recognize the two types of models as endpoints of a continuum. The implications for prediction, however, are important. Predictions can be derived from purely statistical models but may be more robust and general when formulated in an analytical framework, as Livingstone and Imboden (1996) argued. These latter, more analytical models need not be purely deterministic. Analytical models often tend to present single answers as graphs and appear attractive relative to purely empirical models with their large, conspicuous errors. Uncertainty, however, resides in the underlying empiricisms used to parameterize analytical models, and these uncertainties can be profitably projected as in the case of the fishery decision table described above (Table 1).

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Perspective

Given the goal of science as understanding, why accept prediction as an important standard and objective for aquatic science? The traditional reason is that testing of predictions is one means to judge the adequacy of understanding. Given the complexity of aquatic systems, it is easy to overestimate understanding, and predictions allow us to confront our general models and assess their adequacy against reality (i.e., data). There are several additional reasons to value prediction. First, there is little doubt that human-driven changes in aquatic systems will require increased efforts in scientific analysis and predictive management in the future. Second, predictive approaches can be guides for research programs helping to keep attention focused on ultimate objectives and not small problems. Third, if aquatic scientists take the mandate for prediction seriously, there should be sufficient dissatisfaction with our current abilities to foster new and creative approaches.

Predictions are clearly needed for practical reasons. This can easily be understood by considering the problems of water quality and fisheries that dominate the applied concerns of aquatic scientists. Globally, water expropriation for human use is estimated at 54% of accessible runoff (Postel et al. 1996). Such heavy usage implies shortfalls of high-quality water, at least in some areas of the globe. Curiously, even water-rich regions of the world such as the boreal portion of Canada have water quality problems driven by climate change, acid deposition, and ultraviolet exposure, leading to pessimism about the future condition of freshwater ecosystems (Schindler 1998). Hence, predictions of the consequences for water resources of various anthropogenic uses and impacts will remain an important task for aquatic sciences in the foreseeable future (Likens 1992; Postel and Carpenter 1997; Gleick 1998).

A similar list of concerns applies to fisheries where global stocks are heavily exploited and capture fisheries appear to be at a maximum near 100 Mt·year^{-1} (Botsford et al. 1997; Food and Agriculture Organization (FAO) 1998). Fishing interacts with numerous other features of the environment and economy to create enormous variation in fish stocks. While some of the most creative approaches to science and management have evolved from the challenge of managing variable fish stocks, the problems remain difficult. Failures in fishery management have been spectacular, as well documented in the case of Atlantic cod (Walters and Maguire 1996; Myers et al. 1997). While the underlying sources of these failures may reflect political and management problems as much as scientific limitations (e.g., Hutchings et al. 1997), there can be no doubt about the need for better and more predictive science.

Better predictions should have positive consequences for our ability to manage the environment. By forecasting the consequences of current human activity, it may be possible to forestall some of the worst environmental degradation that the future appears to hold. This is the hope of such scientific efforts as the Intergovernmental Panel on Climate Change where current scientific information is used to evaluate the consequences of global warming (Watson et al. 1996). At more local and regional scales, aquatic ecologists will also need to make explicit the consequences of human activity. If connections among society, economy, and ecological systems can be made plain, strong public sentiments for environmental protection should promote better ecosystem management (Folke 1998).

Prediction should also play an important role in research programs. Predictive models reveal important variables, and these can illuminate underlying causal interactions and contribute to theory. Conceptual constructs often arise from attempts to explain empirical regularities. Theories are also confirmed, refined, or discarded based on tests of their predictions. Thus, prediction has a fundamental role in both the establishment and the evaluation of theory.

Predictive objectives for research may also help to discriminate among possible topics for investigation, thereby aiding efficient progress. A predictive orientation keeps research efforts focused on central questions.

Some would argue against the emphasis that I have placed on prediction and argue for an increased emphasis on the identification and study of mechanisms. Without detailed understanding of controlling mechanisms, prediction, in this view, is a false goal. One reviewer of an earlier version of this paper commented that causal understanding is needed "before application of predictive modeling." I agree that mechanistic understanding is important but think that placing a high value on prediction will help the field move more efficiently toward identifying key mechanisms from a larger universe of possible mechanisms for a given problem. I do not mean to discount, however, the value of mechanistic research, and I am not advocating strictly statistical modeling approaches to prediction. An important point here for the reader is that when it comes to scientific approaches and ways of promoting progress, there are many strongly held and apparently opposing views. One goal of this paper is to encourage constructive discussion and to argue that prediction is an aspect of aquatic sciences worthy of deeper inquiry by all, regardless of favored approaches.

Progress is often born from dissatisfaction. I have articulated here the need for prediction, yet currently, the ability to make either general or specific predictions about aquatic systems is very limited and imprecise. If prediction is held as a standard, this limitation should cause dissatisfaction and discomfort among aquatic scientists. This state is often a source of creativity. Advances likely will come from those who cannot abide the current situation and seek alternative, novel pathways. Hence, prediction should foster advances.

I foresee great progress ahead in the ability to measure and study aquatic systems. There is no doubt that new technology is rapidly improving the acquisition of data and the transmission of information. New means for probing oceans, estuaries, lakes, rivers, and streams are becoming widely available. Methodological improvements alone will probably drive significant new discoveries about the nature of aquatic systems. But what if the ability to make predictions does not improve concomitantly over the next couple of decades? This goal seems more tenuous at present and, if not realized, will represent a significant failure.

Predictive improvement will not happen as an accidental consequence of scientific advances. Instead, prediction must become a significant standard for the aquatic science of the future. This change would help orient aquatic research toward developing both a sounder foundation and a more usable science.

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Ecosystem changes and the effects on capelin (*Mallotus villosus*), a major forage species[1]

J.E. Carscadden, K.T. Frank, and W.C. Leggett

Abstract: Capelin (*Mallotus villosus*), an important forage and commercial fish in the Northwest Atlantic, has exhibited dramatic changes in its biology during the 1990s, coincident with extreme oceanographic conditions and the collapse of major groundfish stocks. Commercial exploitation has not been a serious factor influencing the population biology of capelin in the area. The overall consumption of capelin has declined as predator stock abundances have changed. Data on plankton are sparse, but there appears to have been a decline in zooplankton abundance during the 1990s, and at the same time, a phytoplankton index increased. The impact of the changes in the physical environment has been the subject of previous studies and these are reviewed. The relative impacts of four factors, commercial exploitation, predation, food availability, and the physical environment, on the changes in capelin biology are discussed in the context of capelin as a single species and in the context of the ecosystem. The overall patterns suggest the existence of a "trophic cascade" within the distributional range of capelin in the Northwest Atlantic during the 1990s primarily driven by declines in major finfish predators.

Résumé : Dans les années 1990, on a observé chez le capelan (*Mallotus villosus*), important poisson fourrage et commercial dans l'Atlantique nord-ouest, des changements spectaculaires de la biologie, ce qui coïncidait avec des conditions océanographiques extrêmes et avec l'effondrement des grands stocks de poisson de fond. L'exploitation commerciale n'est pas un facteur qui influe de façon importante sur la biologie du capelan dans cette région. La consommation globale de capelan a baissé avec les changements survenus dans l'abondance des stocks de prédateurs. Les données sur le plancton sont maigres, mais il semble s'être produit une baisse de l'abondance du zooplancton dans les années 1990, tandis que l'indice du phytoplancton était à la hausse. L'impact des modifications du milieu physique ont fait l'objet de diverses études, que nous recensons. Nous examinons les impacts relatifs de quatre facteurs : exploitation commerciale, prédation, disponibilité de la nourriture et milieu physique, sur les changements dans la biologie du capelan, dans le contexte de l'espèce elle-même et dans celui de l'écosystème. Les patrons d'ensemble font ressortir l'existence dans les années 1990, dans l'aire de distribution du capelan de l'Atlantique nord-ouest, d'une « cascade trophique » régie principalement par la baisse des principaux stocks de poissons prédateurs.

[Traduit par la Rédaction]

Introduction

The search for a quantitative knowledge of the dynamics of interactions between the physical and biological components of the marine ecosystem and their effect on the dynamics of fish populations forms the foundation of modern fisheries oceanography (Dower et al. 2000). Nowhere has the need for this knowledge been felt more than in eastern Canada. There, major displacements in the fishery and associated dislocations in communities tied to these fisheries occurred over a relatively short time period in the early 1990s when major groundfish stocks collapsed to historic lows.

At the same time, the physical environment of the Northwest Atlantic became extreme and was characterized by prolonged below-normal sea temperatures. It has proved difficult to disentangle the role of fishing and environmental factors in these changes in stock abundance. Debate over which predominated continues (Lilly et al. 1999 and references therein). The importance of developing a fuller understanding of these dynamics and their role in shaping the events of the recent past in the Northwest Atlantic ecosystem remains high.

Most of the scientific debate over the relative importance of fishing and environment has been focused on species of commercial importance (Lilly et al. 1999). Less attention has been given to coincident changes in lightly exploited species, largely due to the inadequacy of meaningful time series of quantitative data and directed research. In this paper, we examine the causes of coincident and profound changes in the population biology of capelin (*Mallotus villosus*), a key component of the Northwest Atlantic ecosystem that has been the focus of a limited commercial fishery and several basic research initiatives.

Capelin is a small, silvery member of the Osmeridae. It is a cold-water, pelagic, schooling species inhabiting Arctic and sub-Arctic zones in the Atlantic and Pacific oceans. In the Newfoundland area, there are believed to be four stocks

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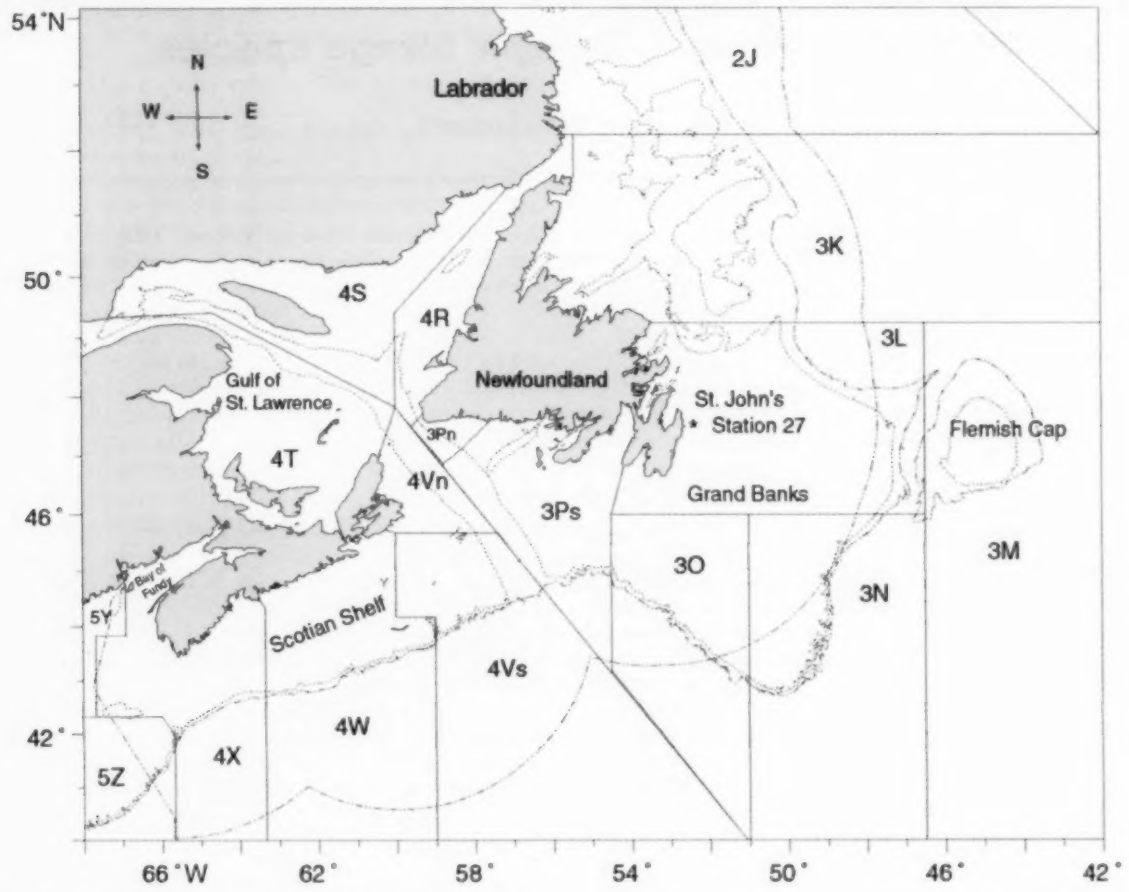
Fig. 1. Map showing locations in the Northwest Atlantic mentioned in the text.



(Nakashima 1992): Northwest Atlantic Fisheries Organization (NAFO) SA2 + Div. 3KL, Div. 3NO, Div. 3Ps, and Div. 4RST (Fig. 1). Historically, the centre of abundance and distribution in the Northwest Atlantic has been in Div. 2J3KL. Capelin spend most of their lives offshore. Spawning occurs in June and July and is coincident in all stocks. Only the Div. 3NO stock spawns offshore; all other stocks move inshore to spawn on beaches (Carscadden et al. 1989).

Capelin typically mature at 3 or 4 years of age (Winters 1982), and these age groups dominate the spawning population. Postspawning mortality has been considered near complete (Carscadden et al. 1985), but recent evidence indicates that postspawning survival may sometimes be as high as 50% (Shackell et al. 1994). Capelin populations are typified by high recruitment variability (Leggett et al. 1984), and with few age-classes in the mature population, this creates the potential for large changes in biomass over short time periods.

Capelin have also exhibited changes in their biology at about the same time as the recent groundfish collapse and the extreme environmental conditions. The timing of the changes roughly corresponded to the 1990s, and in Table 1, we have provided a brief, qualitative description of the biological characteristics in the 1990s and the period prior to the 1990s.

In brief, a major change in distribution, timing of spawning, and average body size of capelin occurred during the 1990s (Frank et al. 1996; Carscadden et al. 1997). Changes in predation due to collapses of major groundfish stocks are likely to have reduced natural mortality. Recruitment does not appear to have changed appreciably during the 1990s, but the estimates are uncertain.

In this paper, we describe these pre- and post-1990 characteristics of capelin in more detail and explore them in relation to four factors that might have an impact on the population biology of capelin. Overexploitation has been cited as a contributing factor in the groundfish collapse. Because changes in capelin biology occurred coincident with the collapse of groundfish stocks, we examine the effect of fishing mortality.

Given the changes in predator abundances in the Northwest Atlantic, we evaluate the hypothesis that changes in distribution, abundance, and mortality result from predation.

Although data are limited, we investigate the hypothesis that changes in food availability underlie the changes in population mean body size and recruitment. Given the broad-scale changes in ocean climate, we also evaluate the hypoth-

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Table 1. Characteristics of Northwest Atlantic capelin populations in the 1990s relative to earlier time periods.

	Prior to 1990 (baseline)	After 1990
Distribution	Centred in Newfoundland	Southward shift from Labrador; expansion to Flemish Cap (east) and Scotian Shelf (southwest)
Growth	Population mean body size large	Population mean body size small
Time of spawning	June	Late July – August
Natural mortality	High	Low
Recruitment	Variable	Variable and uncertain

esis that changes in the physical environment account for the pre- and post-1990 characteristics observed. Finally, we discuss the changes in capelin biology in the broader context of the ecosystem, with particular emphasis on trophic cascades (Steneck 1998; Pace et al. 1999).

Exploitation

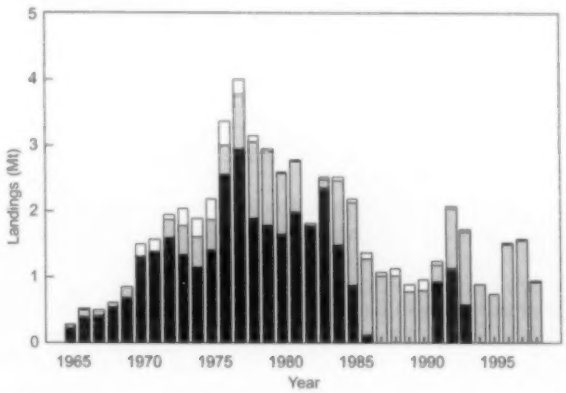
In recent decades, fishing pressure on the world's fisheries has increased sharply. This increase has been most pronounced on top predators such as groundfish. The increasing concentration of fishing effort on planktivorous or forage fishes (sensu Springer and Speckman 1997) is now raising concerns.

Their abundance and schooling nature make forage fish both attractive and vulnerable to fishing. Their importance as food for a wide range of species and as mechanisms of energy transfer to higher trophic levels fuels the arguments that fishing of forage fishes should not occur. The latter concerns emanate from many sources. Those who oppose their exploitation do so because the list of predators ranges from important commercial predators (fishes) to species that sustain ecotourism (e.g., birds and marine mammals). This concern is heightened by the reality that of the top 10 fish species exploited worldwide, small pelagic fish constituted less than 60% of the total landings in 1973 but approximately 75% in 1993 (Fischer et al. 1997). Pauly et al. (1998) concurred and reported that over the last 45 years, global fish landings have shifted from large piscivorous fishes to small invertebrates and planktivorous fishes. They contend that this practice of "fishing down the food web," usually without an increase in total catch, is unsustainable and will likely compromise ecosystem stability. Steneck (1998) noted that a reduction in the populations of top predators often results in an increase in prey populations, or a trophic cascade. This in turn presents the possibility that a new directed fishery may emerge on the prey species released from predation. This fishing of trophic cascades does not promote sustainable harvests and is viewed as a sign of ineffective management (Steneck1998).

In the Northwest Atlantic ecosystem, capelin have been the subject of a directed commercial fishery since the early 1970s and are a key forage species. Winters and Carscadden (1978) estimated that capelin contributed in excess of 4.6 Mt annually to the diets of cod, seals, and whales prior to 1970. Seabirds and many other finfish species are also known to forage extensively on capelin (Jangaard 1974). Consequently, it is not surprising that the wisdom of fishing capelin might be questioned.

Prior to the 1950s, 20 000 – 25 000 t of capelin was taken annually in Newfoundland for bait and fertilizer and to a lesser extent food for dog teams (Templeman 1968). Inshore landings declined considerably until the early 1970s, when a directed offshore foreign fishery began. During the late 1970s, the offshore fishery declined and an inshore fishery developed to supply roe-bearing females to a Japanese market. During the 1980s, the fishery was dominated by domestic inshore catches, and by 1992, the offshore fishery had been eliminated.

Fig. 2. Landings of capelin in Canada from SA2 + Div. 3KLNO (open bars), Iceland (grey bars), and the Barents Sea (solid bars) from 1965 to 1998.



On a global scale, the catches of capelin in Canadian waters are relatively small. Norwegian and Icelandic capelin fisheries have each routinely landed upwards of 1 000 000 t annually (Fig. 2). Landings in Norway accounted for an average of 39% (range 20–55%) and 14% (range 12–16%) of the total stock estimate between 1973 and 1986 and between 1990 and 1993, respectively (fishing was closed between 1986 and 1990) (tables 4.2.1 and 4.3.2.2. in Anonymous 1999*a*). For Iceland, landings averaged 43% (range 20–61%) of the total biomass estimate from 1978 to 1998 (table 5.7.1 in Anonymous 1999*a*). Both fisheries exploit primarily prespawning and spawning fish.

Since 1979, Canadian management policies specified that removals by a fishery should be no more than 10% of the spawning stock biomass. Although this exploitation rate was arbitrary, it was considered conservative and was set low to reflect the central role of capelin as a forage species and the uncertainty concerning both recruitment rates and abundance, which, at the time, were believed to be low. Shelton et al. (1992) examined this management strategy and reported that the catch between 1982 and 1989 in the Div. 3L stock (now

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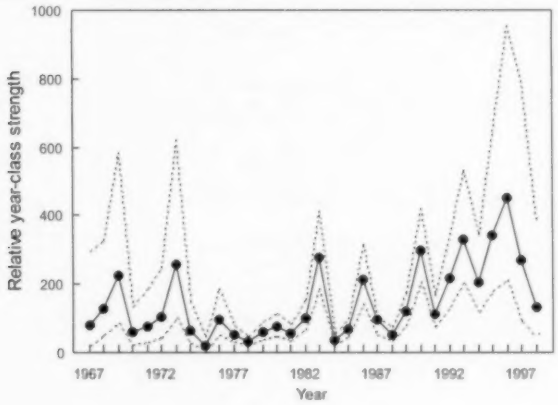
Fig. 3. Estimates of relative strength of SA2 + Div. 3KL capelin year-classes, 1967–1998. The dotted lines surrounding the estimates are 95% confidence intervals.



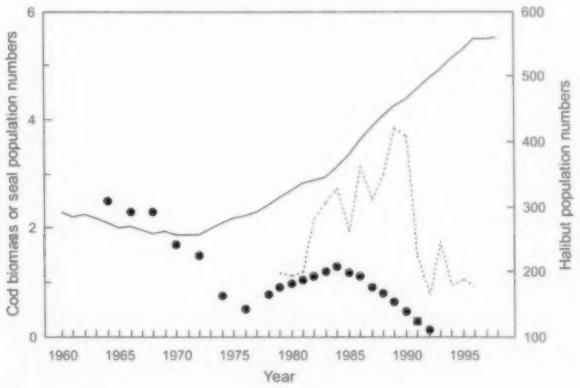
part of the SA2 + Div. 3KL stock) averaged 4.3% of the estimated mature biomass.

Canadian catches in the 1980s were consistently lower than in the 1970s when fishing mortality rates (F) were estimated to be below 0.1 (Carscadden and Miller 1981). Leggett et al. (1984) and Carscadden et al. (2000) developed and verified a recruitment model for capelin. The verification revealed that 25% of the recruitment variation in capelin in SA2 + Div. 3KL during the interval 1966–1990 was explained by abiotic variables. No significant stock–recruitment relationship was found, and the survival index used in the analysis reflected predominantly abiotic effects on year-class abundance.

The relative impact of the capelin fishery is more difficult to assess for the 1990s (Carscadden and Nakashima 1997). Nevertheless, estimates of relative year-class strength, derived from several independent sources and combined into a multiplicative model (Fig. 3; Anonymous 1999*b*), indicate that year-class strengths during the 1990s have been at least as strong as those observed during the 1980s, while total landings have been lower (Fig. 2).

To our knowledge, bycatch of capelin in other directed fisheries has never been cited as a major concern. The only fishery that could potentially take significant quantities of capelin as a bycatch is the shrimp fishery, which uses fine-meshed gear. Indeed, Frank et al. (1996) used bycatch of capelin in the Flemish Cap shrimp fishery as evidence that capelin had moved into the area during the early 1990s. To assess the impact of the shrimp fishery in Div. 2J3K, we noted that the highest bycatch rates of capelin were recorded in 1989, during the period 1987–1994 (Carscadden 1996). From observer data (D. Kulka, Department of Fisheries and Oceans, St. John's, NF A1C 5X1, Canada, personal communication), we calculated the average catch rate of capelin to be 20.9 kg·h^{-1}. According to NAFO catch and effort statistics (Anonymous 1989), Canadian and foreign vessels spent a total of just over 16 000 h fishing shrimp in Div. 2J3K in 1989. This would yield a total of approximately 343 t of capelin as bycatch. This corresponds to 0.70% of the commercial capelin catch in Div. 2J3K and 0.33% of the total commercial catch in the SA2 + Div. 3K stock in 1989.

Fig. 4. Total population estimates (millions) of harp seals in the Northwest Atlantic (solid line) (formulation 1 from Stenson et al. 1999). The circles denote estimates of 3+ biomass (Mt) for Div. 2J3KL cod. Estimates for 1978–1992 were obtained from table 30 and for 1964–1976 from fig. 26 in Bishop et al. (1993). The dotted line shows estimates of Greenland halibut numbers (millions), ages 4–10, NAFO Div. 2J3K, from table 18 in Brodie et al. (1997).



We conclude that there is no evidence that overexploitation of capelin has occurred at any point in the history of the fisheries in SA2 + Div. 3KL where most of the fishing has occurred. Indeed, when contrasted with other pelagic fisheries (Beverton 1990), the fishing pressure exerted on capelin in Canadian waters must be judged to have been minimal.

Predators

The abundances of the most important predators of capelin have changed dramatically in the time period for which population estimates are available. Harp seal abundance varied between about 1 900 000 and 2 300 000 animals between 1960 and 1977 but then began to increase until by the mid-1990s, the population was in excess of 5 000 000 animals (Stenson et al. 1999).

Cod biomass declined from approximately 2.5 Mt in the mid-1960s to approximately 500 000 t in the mid-1970s. The population then showed a partial recovery to a peak of approximately 1.3 Mt in 1984 before collapsing in the 1990s (Fig. 4). The cod biomass in 1998 was estimated between 50 000 and 150 000 t (Anonymous 1999*c*).

Greenland halibut in the length range of 30–59 cm, which corresponds to ages 4–10 (Bowering 1983), feed heavily on capelin. Population vectors for Greenland halibut are available only back to the late 1970s. Trawl survey abundance of the 4–10 age groups in Div. 2J3K peaked at approximately 4.22×10^8 in the mid- to late 1980s before declining to about 1.80×10^8 individuals in 1996 (Brodie et al. 1997).

American plaice, another predator of capelin, experienced a similar decline. The 1995 spawning stock biomass was estimated to have been 95% lower than the mid-1980 levels (Anonymous 1998). The abundance of Atlantic salmon has also declined to historical lows over the same interval (Anonymous 1999*d*). Time series of changes in the abundance or biomass of seabirds and whales are not available.

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Fig. 5. Changes in annual consumption of capelin by cod (solid bars) and harp seals (open bars) for selected years between 1964 and 1996. Estimates of consumption by cod are based on the assumption of a 1:1 ratio between cod biomass and capelin consumed. Estimates for harp seals are based on the assumption that capelin consumption is proportional to harp seal abundance. The population vector for harp seals used is from Fig. 4, and the starting estimate is the known consumption and population estimate in 1996.

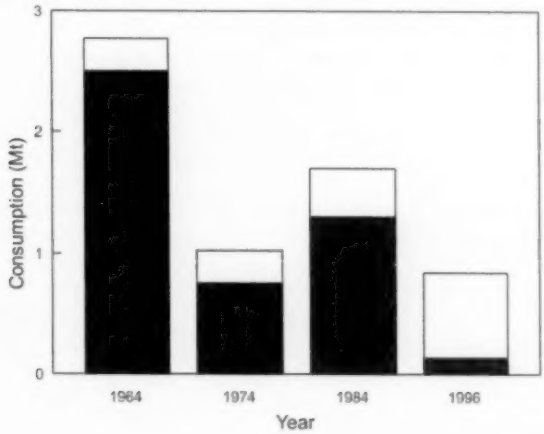
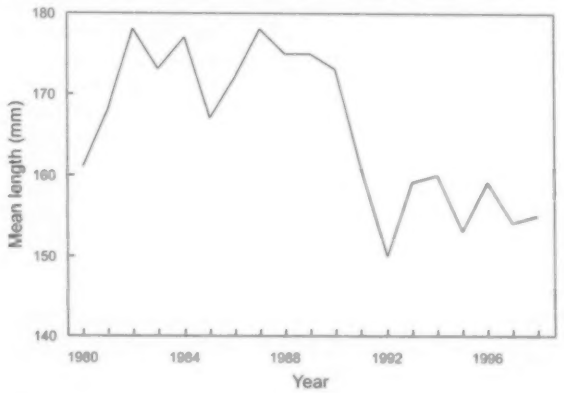


Fig. 6. Mean standard length of mature capelin (sexes combined) from 1980 to 1998 in Div. 2J3KL. All data originated from the commercial inshore fishery except for 1994 and 1995, when the landings were very low due to small fish sizes. Data for 1994 and 1995 were obtained from inshore scientific sampling of spawning beaches. (B. Nakashima, Department of Fisheries and Oceans, St. John's, NF A1C 5X1, Canada, personal communication).



Winters and Carscadden (1978) estimated that the ratio of annual capelin consumption by cod to cod biomass approximates 1.0. Minet and Perdou (1978) provided independent estimates ranging from 0.76 to 1.27. Using the Winters and Carscadden (1978) estimate as an approximate midpoint, this implies that the consumption of capelin has declined from about 2.5 Mt in the 1960s to approximately 100 000 t in the late 1990s, a reduction of 96%. Even during the partial recovery of cod during the 1980s, consumption of capelin would have been only about one half the consumption in the 1960s. Turuk (1978) estimated the ratio of capelin consumption to cod biomass to be much higher at 2.38. Assuming this estimate to be valid, the reduction in consumption of capelin by cod in the 1990s relative to the 1960s could be as great as 5.6 Mt annually.

In recent years, harp seals and their prey consumption have been under intensive study. During 1996, harp seals were estimated to have consumed about 710 000 t of capelin in NAFO Div. 2J3KL (Hammill and Stenson 2000). For harp seals, prey consumption is proportional to predator abundance (Hammill and Mohn 1994; Stenson et al. 1997). The harp seal population between the mid-1960s and early 1980s did not change very much and was about 40% of the estimates from the mid-1990s. Therefore, we conclude that the increase in capelin consumption by harp seals between the earlier period (1960–1980) and the mid-1990s has been on the order of 400 000 t annually.

The annual consumption of capelin by Greenland halibut in the 1980s, prior to their increase in abundance in the late 1980 – early 1990 period, was estimated to range from 100 000 to 200 000 t (Bowering and Lilly 1992). The current abundance of Greenland halibut approximates that of the early 1980s, and therefore, the consumption of capelin is probably about the same.

Times series of the abundance or biomass of seabirds and whales are not available. However, Brown and Nettleship (1984) estimated that capelin consumption by seabirds was 250 000 t·year^{-1}, similar to an estimate of 234 000 t for the mid-1980s (W. Montevecchi, Department of Psychology and Biology, Memorial University of Newfoundland, St. John's, NF A1B 3X9, Canada, personal communication). Winters and Carscadden (1978) estimated that at virgin stock levels, fin and minke whales consumed about 400 000 t of capelin annually. A more recent estimate of consumption by humpback, fin, minke, pilot, and sei whales and harbour porpoises indicated that about 700 000 t of capelin was eaten annually during the 1985–1987 period (Bundy et al. 2000). Since these animals have slow reproductive rates, we have assumed that neither their populations nor their consumption of capelin have changed substantially over the time period in question.

Given the above, we conclude that the overall consumption of capelin during the 1990s has declined. Assuming Winters and Carscadden's (1978) ratio of prey consumption to cod biomass, we estimate the net reduction in capelin consumption by its major predators to be on the order of 2 Mt annually when compared with the consumption during the mid-1960s. While the estimate is subject to numerous assumptions, the predominance of consumption by cod, relative to the combined consumption by all other predators for which there are data, renders this estimate robust. The historical trends in consumption of capelin by cod and harp seals are illustrated in Fig. 5 where estimates of consumption are presented for 4 years spanning four decades (1964, 1974, 1984, and 1996).

We note that this is coincident with two important features of capelin during the 1990s, namely the production of several strong year-classes in the SA2 + Div. 3KL stock (Fig. 3) and a decrease in the average body size of capelin (Fig. 6), perhaps as a consequence of increased density dependence.

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A similar pattern of decreased body size coincident with increased stock abundance has been reported for Icelandic capelin (Anonymous 1999*a*).

Food availability

Capelin are planktivores, with copepods, euphausiids, and amphipods comprising the main diet items (Gerasimova 1994; Gjosaeter 1998). The relative importance of each component in the diet of Barents Sea capelin varies with season, area, predator size, and year (Gjosaeter 1998). Feeding data in the Newfoundland area are not extensive; however, similar conclusions can be drawn from the limited data. On the Grand Banks, the spring diet of immature capelin is dominated by copepods and that of mature capelin by euphausiids. Together, these prey taxa constitute 60–80% of the diet (Gerasimova 1994). In the Labrador area, the autumn capelin diet was dominated by copepods and amphipods, and on the southwest Newfoundland coast, amphipods and euphausiids were most important in the winter diet (Chan and Carscadden 1976).

The longest time series that quantifies zooplankton concentrations in Canadian waters is the continuous plankton recorder (CPR) data (Sameoto et al. 1996), and although it started in 1956 and continues, there are large data gaps that vary between areas. Data are available from both the eastern Scotian Shelf and the Grand Banks, and the patterns of *Calanus finmarchicus* stages 1–4 and total euphausiids from both areas are similar. Generally, the earlier parts of the series, that is, from the 1960s and 1970s, are characterized by above-average concentrations, in contrast with the 1990s, when concentrations of these zooplankters were below average (D. Sameoto, Department of Fisheries and Oceans, Dartmouth, NS B2Y 4A2, Canada, personal communication).

A colour index (greenness) is also derived from the CPR data, and this index is interpreted as an index of phytoplankton abundance. Like the zooplankton, the trends between the eastern Scotian Shelf and the Grand Banks were similar to each other. However, the temporal trends in the phytoplankton were the opposite of those of the zooplankton. For phytoplankton, the earlier period exhibited below-average phytoplankton abundance but the 1990s exhibited above-average abundance (D. Sameoto, Department of Fisheries and Oceans, Dartmouth, NS B2Y 4A2, Canada, personal communication).

Although there are no other direct measures of zooplankton abundance over a long time period, stomach content data can provide insights into trends in prey availability. M. Hanson (Department of Fisheries and Oceans, Moncton, NB E1C 9B6, Canada, personal communication) has found that euphausiids never represented less than 5% of prey weight for Atlantic cod (30-59 cm) in the southern Gulf of St. Lawrence during 1956–1987. In contrast, in 1990–1993, 1995, and 1999, only trace amounts of euphausiids were found and a low level of euphausiid consumption was reported in 1994. Although these results do not necessarily indicate low euphausiid abundance, we note that this low occurrence of zooplankton in cod diets in the southern Gulf of St. Lawrence during the 1990s is coincident with the decreased abundance of zooplankton over both the eastern Scotian Shelf and the Grand Banks.

Skjoldal et al. (1992), Dalpadado and Skjoldal (1996), and Hassel et al. (1991) all reported the existence of inverse relationships between changes in capelin abundance and the biomass of euphausiids in the Barents Sea. In each case, the changes in euphausiid biomass lagged behind the change in capelin numbers. Hassel et al. (1991) also noted that the biomass of krill in the upper 100 m of the Barents Sea in 1985 was much lower in areas where capelin were present as compared with areas where they were absent. They concluded that capelin had the potential to graze down the available zooplankton prey in 3–4 days.

Astthorsson and Gislason (1998) reported that mean weights at age and biomass of capelin were significantly higher in warm years than in cold years. These parameters could not be statistically linked to zooplankton abundance; however, the authors suggested that the positive trends in capelin growth followed those in zooplankton. Leggett et al. (1984) developed a model to explain observed changes in the recruitment success of capelin in eastern Newfoundland. One of the two variables found to contribute significantly to the explained variance in recruitment was the sum of monthly mean temperatures in the 0–20 m depth range for the first 6 months of pelagic existence. The authors interpreted the temperature variable to be a proxy for zooplankton production.

Physical environment

The causes of long-term trends in the ocean climate of the Northwest Atlantic are documented in Mann and Drinkwater (1994). The atmospheric circulation over the North Atlantic is dominated by two features, a subtropical high-pressure system centred over Bermuda and the Azores and a subpolar low-pressure system centred near Iceland. Oscillation in the pressure difference (December–February) between the two systems, reflected in the winter air pressure difference between Ponta Delgada in the Azores and Akureyi in Iceland, has been termed the North Atlantic Oscillation (NAO). A strong, positive difference produces strong northwesterly winds across Newfoundland and Labrador, which bring cold Arctic air into the region in the winter. This produces heavier ice cover, a larger deep cold intermediate layer, and lower surface and bottom temperatures. Minimum anomalies resulting in warm winters and below-normal ice cover occurred during the 1960s. During the 1970s, strong positive anomalies produced above-average ice cover and below-average temperatures. These conditions reappeared in the 1980s and in the early 1990s when they persisted for a longer period. In the mid-1990s the strength of the NAO began to weaken, producing near-average conditions in 1997 and 1998 (Mann and Drinkwater 1994; Drinkwater et al. 1999) (Fig. 7).

These changes are reflected in the depth-integrated water temperatures recorded at a station east of St. John's, Newfoundland (Station 27; 47°31′50″N, 52°35′10″W), occupied on an opportunistic basis since 1946 during scientific research surveys in the area (Fig. 8). Variations in ocean temperatures measured at Station 27 have been shown to be coherent from southern Labrador to the northern Grand Banks (Petrie et al. 1988 Drinkwater et al. 1999).

Many of the changes in capelin biology observed during the 1990s have been linked statistically or circumstantially to the low sea temperatures during the same period. Capelin

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Fig. 7. Anomalies of the NAO index relative to the 1961–1990 mean (Drinkwater et al. 1999). The trend line (solid line) is based on a 5-year running mean.

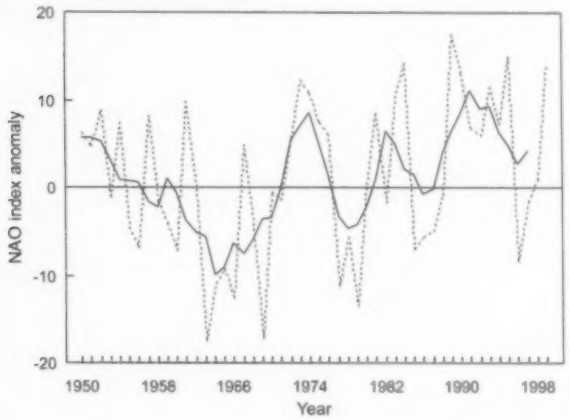


Fig. 8. Vertically integrated temperature (0–176 m) anomalies from Station 27 (Drinkwater et al. 1999). The trend line (solid line) is based on a 5-year running mean.

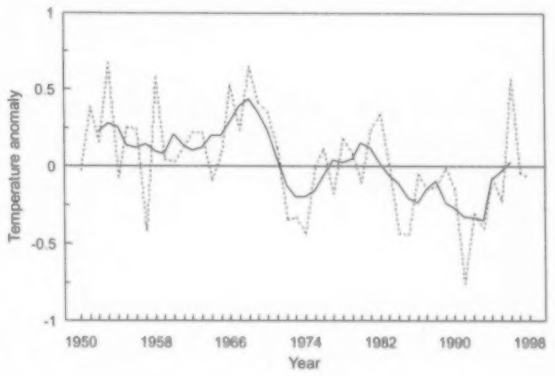
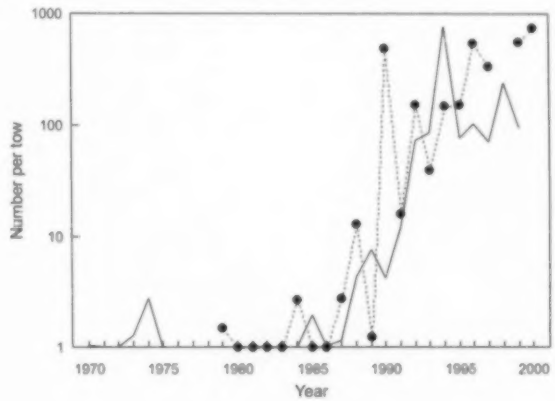


Fig. 9. Mean numbers of capelin per tow for Div. 4VW during spring and summer research vessel surveys. The spring survey began in 1979 and is depicted by circles. The summer survey began in 1970 and is shown as a solid line.



shifted in their normal distribution area in SA2 + Div. 3KL, all but disappearing from the Labrador coast in Div. 2J and occupying an area centred on the northern Grand Banks spanning the boundary of southern Div. 3K and northern Div. 3L. This pattern was consistently observed in a variety of sources including acoustic surveys directed for capelin (Carscadden and Nakashima 1997), bycatch in groundfish surveys (Lilly 1998), 0-group surveys (Anderson et al. 1999 and references therein), and changes in predator diets off the coast of Labrador (Arctic char: Dempson 1995; seabirds: Anonymous 1997). At the same time, capelin appeared in unusually high numbers on the Flemish Cap and eastern Scotian Shelf. All of these unusual occurrences in the 1990s and in previous years (early 1970s and early 1960s) had occurred during cold periods. Some earlier, relatively brief cold periods (e.g., mid-1980s) had not resulted in the appearance of capelin in these unusual areas. Low temperatures were necessary for these excursions but did not always result in such movements (Frank et al. 1996). Capelin were reported on the Flemish Cap until 1997 (Vaskov et al. 1996; Kulka 1998; Vaskov and Berenboim 1998), but there have been no reports since then. In this area, negative temperature anomalies at all depths began in the 1980s and continued into the early 1990s. In 1998, temperatures at the surface were just above normal, temperatures at middepths were just below normal, and temperatures near bottom remained below normal (Drinkwater et al. 1999). On the Scotian Shelf, high capelin bycatches have continued up to 2000 (Fig. 9). Water temperatures exhibited negative anomalies beginning in the mid-1980s and continued until 1998. The waters were warming in the late 1990s, but overall temperatures were below the long-term mean (Drinkwater et al. 1999).

Beach spawning of capelin was as much as 1 month late and average fish lengths were smaller during the early 1990s (Fig. 10). The timing of spawning was negatively correlated with sea temperatures during the maturation phase and mean fish length; thus, colder temperatures and smaller fish lengths were associated with later spawning (Carscadden et al. 1997). Although the same spawning beaches have not been monitored for spawning times since the original study, the timing of spawning at another beach nearby has gradually shifted toward a pattern similar to that of the 1980s (B.S. Nakashima, Department of Fisheries and Oceans, St. John's, NF A1C 5X1, Canada, personal communication). Mean fish sizes have remained small (Fig. 6), but sea temperatures have been returning to the long-term mean. Thus, the gradual shift to spawning that is still slightly later than normal is consistent with the changes in one of the independent variables.

Recruitment variation in capelin has been shown to be related to physical factors, namely the frequency of onshore wind events during the beach residence time of larvae immediately following hatching and surface water temperatures during the first 6 months of pelagic existence (Leggett et al. 1984). In a test of this model, Carscadden et al. (2000) found that later year-classes were successfully predicted only if two outliers (out of 12 year-classes) were omitted from the analysis. When the model was reconstructed using the entire time series (1966–1990), only onshore wind frequency was significant in explaining capelin survival. The model was not tested for year-classes after 1990 because the influences of

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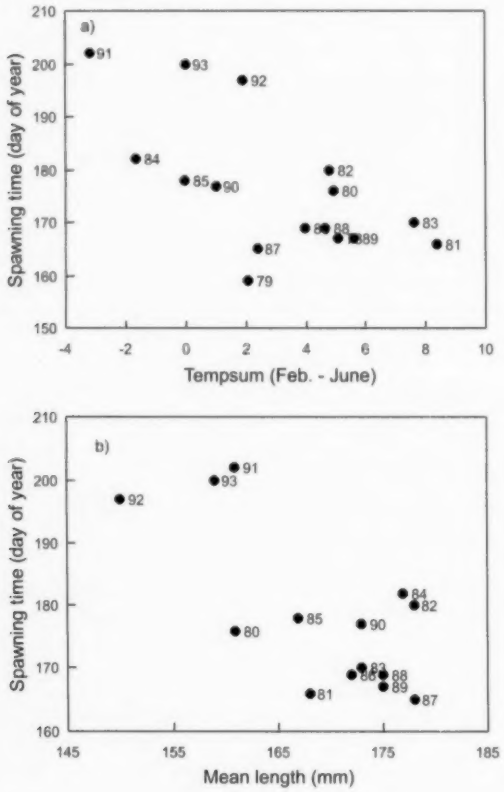
Fig. 10. (*a*) Scatter plot of capelin spawning time versus Tempsum, the mean monthly temperatures at 0–20 m, February–June, from Station 27, 1978–1994, and (*b*) scatter plot of spawning time and mean length of capelin, 1980–1993.



the changes in biological factors in the model were not known. The geographic distribution of the year-classes after 1991 were different from those of the year-classes on which the model was based, and the temperature variable describing sea temperatures during larval drift included rather than excluded the actual spawning periods.

Clearly, the physical environment has a significant impact on several biological characteristics of capelin. Dramatic changes in distribution and spawning times have been linked to temperature changes, and these changes were particularly noticeable in the 1990s. Survival is enhanced by favourable onshore winds during the larval beach residence phase. Although this relationship was not tested for the 1990s, it was significant using a 25-year time series.

Discussion

Significant changes in capelin biology occurred during the recent time period roughly corresponding to the 1990s. We now return to the listing of these characteristics in Table 1 to focus our discussion on the differences between the 1990s and earlier periods and how they relate to and might be influenced by other changes in the biological and physical components of the ecosystem.

We conclude that exploitation of capelin has not been a serious factor influencing the population biology of capelin in SA2 + Div. 3KL where directed fishing has occurred for nearly 30 years. Fishing mortalities have been low even during the offshore foreign fishery of the 1970s when catches were higher than during the 1980s and 1990s. On average, annual catches in the Northwest Atlantic have been a fraction of the catches around Iceland and in the Barents Sea. Removals by humans have been low when compared with removals by predators, especially when predator stocks were much higher historically. As an example, peak catches in the mid-1970s in the entire SA2 + Div. 3KLNO area were about 360 000 t compared with an estimated removal by cod in excess of 2 500 000 t. Catches since then have averaged much less than the mid-1970s' peak and at the same time, predation has declined with the decline of many major capelin predators.

Large-scale changes in capelin distribution during the 1990s have been linked to below-normal water temperatures. Similar excursions to the same areas were also observed in earlier cold-water periods (Frank et al. 1996). However, capelin population numbers have also increased during the 1990s, raising the question of whether emigration to unusual areas has occurred because of increased population density, similar to that reported for other species (Marshall and Frank 1995). While we cannot eliminate density entirely as a factor contributing to the unusual distributions during the 1990s, we suggest that the physical environment is probably more important, based on the following reasons.

First, capelin appeared on Flemish Cap, eastern Scotian Shelf, and the Bay of Fundy during other cold periods. Although population estimates of capelin are not available for these earlier time periods, it is unlikely that capelin populations were as abundant or more abundant than they are presently, due to the impact of heavier predation in earlier periods (see later discussion).

Second, changes in timing of migration and (or) distribution have also been observed in other areas. In Iceland, when capelin are not detected during acoustic surveys in the usual area at the expected time, the acoustic survey is repeated to accommodate this variation in capelin behaviour. The Icelandic capelin stock has maintained high biomasses and produced high yields since the early 1980s (Vilhjalmsson 1994). In the Barents Sea, capelin spawning areas vary east or west along the Norwegian–Russian coast. This displacement has been linked to distribution prior to spawning, which in turn varies depending on whether water temperatures are warm or cold (Gjosaeter 1998). In the Newfoundland–Labrador area, several acoustic surveys in the normal offshore distribution areas for capelin have failed to detect significant quantities of capelin between 1991 and 1996, suggesting changes in caplin distribution, timing of migration (Shackell et al. 1994), and (or) schooling behaviour (Carscadden and Nakashima 1997). The most striking example occurred in 1991 when two Canadian surveys (Miller and Carscadden 1991) and one Russian survey (Bakanev 1992) operating sequentially between May and July in Div. 3KL did not find substantial concentrations of capelin in the normal area. That year was the coldest year in the oceanographic record and the first year that capelin spawning was noticeably later. The late spawning resulted in problems in evaluating abundance, but

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the year-class resulting from the 1991 spawning has been estimated to be above average.

Third, two other cold-water species, Greenland halibut and checker eelpout, also increased in abundance on the eastern Scotian Shelf, coincident with the capelin increase and the decrease in bottom temperatures during the 1990s. The historical patterns of abundance in this area were also similar to capelin, with increases in the mid-1970s. Greenland halibut also appeared in the Bay of Fundy during the period of below-normal sea temperatures in the 1960s. We suggest, then, that changes in distribution are most likely due to changes in the physical environment, and in the case of the Newfoundland capelin, the physical conditions were unusually severe in the early to mid-1990s.

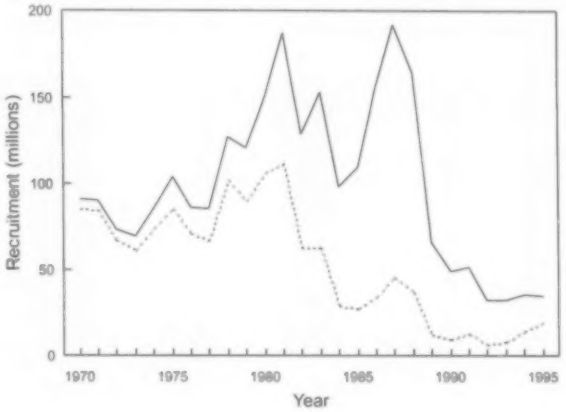
Could the changes in distribution be linked to the changes in predator abundance? Total predation pressure has been reduced, and we suggest that it is unlikely that this reduction would result in the large-scale changes in capelin distribution. However, prey are known to alter their behaviour in response to changes in the environment (Lima and Dill 1990), and Carscadden and Nakashima (1997) reported that lower than expected acoustic estimates might be partially explained by changes in capelin behaviour such as schooling. It is possible then that capelin may be behaving differently in their normal distribution area in response to the change from a finfish-dominated to a harp seal dominated predator field.

During the 1990s, the average fish length in the mature population has been smaller than during previous periods. There have been no studies to address this trend, but we suggest that several interacting factors could be operating. Below-normal water temperatures could be directly affecting growth while at the same time affecting productivity of zooplankton. There are indications that zooplankton concentrations on the Grand Banks during the 1990s were lower than in earlier periods. It has been reported (Anonymous 1999*b*) that there are greater proportions of capelin recovering from spawning in the 1990s. This may be due to lower predation pressures by cod. Historically, cod migrated inshore during the capelin spawning migration and fed heavily on capelin during and after capelin spawning (Akenhead et al. 1982). Larger numbers of recovering capelin could also result in a further density-dependent effect through competition for zooplankton, especially during the autumn.

The delay in spawning during the 1990s has been negatively correlated with both water temperature prior to spawning and average fish size (Carscadden et al. 1997). Maturation progresses rapidly during the spring period (Carscadden et al. 1997), and therefore, the physiological process of maturation would be expected to be regulated by temperatures during this period, as it is for other species (Pacific herring: Hay 1985; cod: Kjesbu 1994). The effect of fish size on spawning is not clear. In Norwegian spring-spawning herring, smaller fish also spawn later, and Slotte (1998) attributed this to lower energy levels. Larger fish are able to store more energy, swim faster, and have a lower metabolic rate and can therefore arrive at the spawning grounds earlier (Slotte 1998). This may also be the case for capelin.

Capelin year-class abundance has been high during the 1990s and the frequency of good year-classes has increased. During 1979–1989, only two (1983 and 1986) strong year-classes were produced whereas there have been six strong

Fig. 11. Reconstructed population estimates of cod recruitment (age 1) with (solid line) and without (dotted line) the effects of grey seal predation.



year-classes between 1990 and 1998. The trend is consistent with the overall decline in predation, which became most acute during the 1990s. Most major finfish predators have been very low in abundance during the 1990s, but the major predator, cod, is at a historical low. Consumption by harp seals has doubled between the early 1980s and mid-1990s, but this increase has not compensated for the reduction in predation due to the decline in groundfish stocks. The reduction in predation has probably occurred on both prespawning and postspawning capelin. We suggest that reduced predation on postspawning fish has resulted in increased spawning survival, while reduced predation on juveniles has resulted in increased recruitment. The latter might be compared with the increased predation by a growing grey seal population on the juveniles of the Div. 4VsW cod stock and the resulting effect on recruitment (Fig. 11) (Mohn et al. 1998). In the case of capelin, seal predation is not having a detectable impact because the reduction of predation by cod is much greater.

The changing structure of the ecosystem may be a factor in the performance of the original recruitment model and the update (Leggett et al. 1984; Carscadden et al. 2000). Although one density-independent factor, wind, was still important to early larval survival, the link between the early life history phase and recruitment to the mature stock may have become more tenuous as predation pressure was more relaxed. In the updated version of the model (Carscadden et al. 2000), temperature during the early pelagic phase was not a significant variable in explaining recruitment variation. Changes in this sort of reanalysis are not unusual (Myers 1998); however, if predation is significantly affecting survival and recruitment, we suggest that future retesting of the model should include a factor for predation, especially by the major predators such as cod and seals. Although temperature was reduced in importance during the reanalysis, we also recommend that it be included in any future considerations. We base this on the observation that during the reanalysis, 10 out of 12 year-classes were successfully predicted using the original model that used two independent variables, wind and temperature. Furthermore, links between capelin abundance

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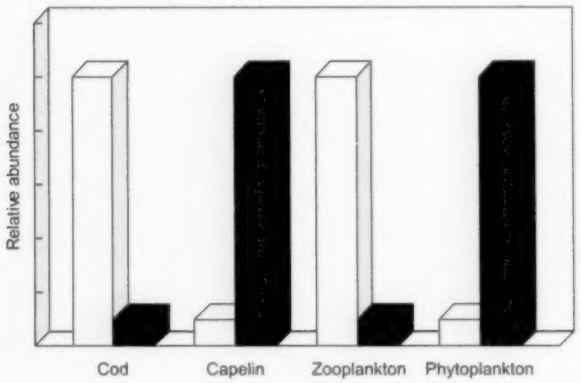
Fig. 12. Schematic representation of the relative changes in abundance (not to scale) of different trophic levels in the Newfoundland–Labrador area during the 1990s (solid bars) and prior to the 1990s (open bars) illustrating the trophic cascade.



and temperature have been reported in both the Barents Sea (Skjoldal et al. 1992) and Iceland (Astthorsson and Gislason 1998).

The abundance of a number of species at different trophic levels has changed dramatically, especially during the last decade, and we hypothesize that a trophic cascade has occurred. Pace et al. (1999) described cascades "as reciprocal predator–prey effects that alter the abundance, biomass or productivity of a population, community or trophic level across more than one link in a food web." In the Northwest Atlantic, we have witnessed the collapse of the major finfish consumer of capelin, Atlantic cod, along with similar declines in other capelin predators including American plaice and salmon. Only one important capelin predator, for which there are historical population vectors and feeding data, has increased. This is the harp seal; however, the evidence indicates that the consumption of capelin by seals has not compensated for the decline in consumption by finfish. Capelin abundance has increased, with improved annual recruitment and several strong year-classes during the 1990s. Zooplankton is lower in abundance, while primary producers are higher in abundance. Conceptually, there appears to be a trophic cascade within the distributional range of capelin in the Northwest Atlantic during the 1990s primarily driven by declines in major finfish predators (Fig. 12).

The scenario that we have described is somewhat simplistic, and several points require amplification and some may be viewed as potentially fruitful areas of future research. The conceptual model that we have described is highly dependent on the abundance estimates at each trophic level. The uncertainties in the abundance and changes over time increase further down the food chain. There is little doubt that the major finfish predators have decreased while harp seals have increased over the last few decades. The capelin estimates are derived using data from several independent sources, which show similar trends. However, the estimates have large statistical uncertainties, and there are two other sources of information, namely acoustic surveys and opinion surveys of capelin trap net fishers, that are not in agreement with the trends in stock status reports (Anonymous 1999*b*). The zooplankton data and greenness index are from CPR data, which are opportunistic data collections along fixed shipping routes and which exhibit large data gaps.

The physical environment during the 1990s was severe, and the possible effects on productivity, especially at the lower trophic levels, must be considered. In Icelandic waters, Astthorsson and Gislason (1998) reported that zooplankton and capelin growth and biomass were higher in warm years and lower in cold years. There is no consensus on the mechanisms affecting zooplankton and phytoplankton production. For example, some authors suggest bottom-up control (Dickson et al. 1988) whereas others (Colebrook 1986) argue top-down control with zooplankton grazing controlling the phytoplankton bloom. Some of the possible influences of the physical environment might be addressed by a closer examination of the temporal sequence of events.

Our hypothesis involves a top-down cascade, beginning with the decline of top predators. This implies that a time lag before the impacts would be felt further down the food chain. The presence of a time lag might be possible to detect, especially for the cod–capelin link, with a more detailed examination of the decline of length groups of cod most likely to prey on capelin in relation to the timing of the capelin increase. Without prior knowledge of the degree of predator decline necessary to have an impact on capelin abundance and given the known environmental effects on capelin recruitment, a modelling approach would probably be very useful. The empirical evidence from the Barents Sea (Skjoldal et al. 1992; Dalpadado and Skjoldal 1996) showing a lagged effect of capelin on zooplankton supports both our hypothesis of a trophic cascade in the Northwest Atlantic as well as further research to detect a temporal connection.

We have examined links with capelin as the focus because it is the dominant forage species in the area. However, shrimp, another forage species, increased in abundance in the early 1980s and the 1990s. Lilly et al. (2000) examined the cod–shrimp relationship and concluded that the earlier increase was probably not related to changes in cod, but the increase during the 1990s could be explained in part by the decrease in the cod population. The predator–prey relationship in the Newfoundland–Labrador area is not simple, since other small-bodied fish, such as Arctic cod and sand lance, are potential competitors of capelin and (or) prey for cod. There is very little information on either of these species.

Investigators of other boreal marine ecosystems have demonstrated the complexity of the predator–prey interactions. In Iceland, cod growth depends on the abundance of capelin, but for capelin, environmental conditions rather than cod predation affect capelin biomass. For the shrimp population, mortality due to juvenile cod predation is important (Stefansson et al. 1998). Dramatic changes in the Barents Sea during the last four decades have altered the predator–prey complex and the population dynamics of the major species. The Norwegian spring-spawning herring stock collapsed during the 1960s due to overfishing. With the collapse of a stock estimated at about 10 Mt, the predator–prey system became dominated by cod and capelin. During the 1980s and 1990s, the herring stock recovered to historical levels, and recent research has shown that when strong herring year-classes occur, the juvenile herring prey heavily on capelin and have a significant impact on capelin recruitment (Gjosaeter and Bogstad 1998).

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While the predator–prey interactions in boreal marine ecosystems are complex, it is clear that cod and capelin are prominent in all cases. Thus, although our approach may be simplistic, we have concentrated on the dominant species in the ecosystem and we view it as a first step in examining the more complex interactions. Knowledge of a key forage species such as capelin without a fishing effect provides valuable insights into the response of a single species to both environmental and predator perturbations and its role in the ecosystem. In his review of marine ecosystem management, Larkin (1996) noted that a major difficulty in modelling ecosystems is their complexity. Only small errors in the estimation of various components in an ecosystem can result in large errors in the simulated result. However, even if ecosystem models such as the trophic cascade framework may not be able to predict the variations in abundance of individual species, they can raise awareness of the interdependencies between trophic levels and provide insights into large-scale changes.

Pauly et al. (1998) reported that the practice of "fishing down the food web" was most noticeable in ecosystems in the northern hemisphere. To date, the situation in the Newfoundland–Labrador area does not seem to fit that generalization. Capelin, the major forage fish species, is not overfished. Fishing effort has recently increased on shrimp and crab in the area, but there is no evidence that overfishing is occurring. However, if fishing down the food web results in unstable ecosystems as Pauly et al. (1998) contended, then there is a strong argument to continue a precautionary approach to fishing forage species in this area. Adherence to this should result in a faster recovery to an ecosystem with a higher biomass of predators, assuming that such a recovery is possible.

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Behaviour in flow: perspectives on the distribution and dispersion of meroplanktonic larvae in the water column[1]

Anna Metaxas

Abstract: For marine benthic invertebrates with meroplanktonic larvae, the relative importance of hydrodynamics and swimming behaviour in determining larval dispersal in the water column, particularly at small spatial scales, has not been determined. In the field, larval aggregations recorded at physical and biological discontinuities in the water column were attributed to hydrodynamics. Similar aggregations obtained in the absence of flow in the laboratory indicate a potentially significant role of behaviour. At large spatial scales, larval distribution in the plankton is mainly regulated by horizontal advection. However, the ability of larvae to behaviourally regulate their position at scales of micrometres to metres when exposed to turbulent fluid motion in the water column, as evidenced in the benthic boundary layer, is unknown. Evaluation of swimming in turbulent flows in the water column is an intriguing area of research, which involves several constraints. In the field, quantification of behaviour is limited by low success in tracking larvae and lack of appropriate observational tools. In the laboratory, the generation and quantification of flow regimes that are representative of those in the field remains a challenge. An approach that integrates biological and physical measurements within realistic ranges is necessary to advance our understanding of larval dispersal.

Résumé : Pour les invertébrés benthiques marins à phase larvaire méroplanctonique, on n'a pas déterminé l'importance relative de l'hydrodynamique et du comportement de nage dans la dispersion des larves dans la colonne d'eau, particulièrement à de petites échelles spatiales. Sur le terrain, les rassemblements de larves observées à des discontinuités physiques et biologiques de la colonne d'eau ont été attribuées à l'hydrodynamique. Des rassemblements similaires obtenus au laboratoire en l'absence de mouvement de l'eau indiquent que le comportement peut jouer un rôle notable. À de grandes échelles spatiales, la distribution des larves dans le plancton est principalement régie par l'advection horizontale. Toutefois, on ne connaît pas l'aptitude des larves à agir par le comportement sur leur position à des échelles allant du micromètre au mètre quand elles sont exposées à des mouvements turbulents dans la colonne d'eau, comme on l'a observé dans la couche limite benthique. L'évaluation de la nage dans des écoulements turbulents dans la colonne d'eau est un domaine de recherche déroutant qui doit tenir compte de diverses contraintes. Sur le terrain, la quantification du comportement est limitée par le faible succès du pistage des larves, et par l'absence d'outils appropriés d'observation. Au laboratoire, la reconstitution et la quantification de régimes d'écoulement représentatifs de ceux du milieu naturel constituent encore un défi. Une approche intégrant les mesures biologiques et physiques dans des plages réalistes nous est nécessaire pour mieux comprendre la dispersion des larves.

[Traduit par la Rédaction]

Introduction

For marine benthic invertebrates with meroplanktonic life cycles, the importance of larval supply in determining the spatial distribution of adult populations is well established (Gaines et al. 1985; Minchinton and Scheibling 1991). However, despite a considerable increase in our understanding of the planktonic larval stages during the last two decades (for a review, see McEdward 1995), the relative importance of factors that determine survival and dispersal while larvae are in the plankton remains elusive (Young and Chia 1987; Rumrill 1990; Young 1995). Several studies have measured larval abundance and distribution in the field, but most have examined effects of different physical (e.g., salinity, temperature, pressure) and biological (e.g., diet, predation) factors on larval behaviour, survival, and development in the laboratory. At present, extrapolation of results from laboratory to field settings is constrained by our limited knowledge of appropriate scaling factors and of the relative importance of the dominant flow regimes.

The individual roles of hydrodynamics and swimming behaviour in larval displacement in the water column have been studied extensively. In an overview of factors that regulate horizontal dispersal at large spatial scales (1000s to 10 000s of kilometres), Scheltema (1986) concluded that the current regime was of overriding importance. Shanks

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(1995*a*) reached a similar conclusion in his evaluation of the studies on cross-shelf transport (100s to 1000s of kilometres) of invertebrate larvae. Focusing on much smaller scales (millimetres to metres), Young (1995) provided a comprehensive review of patterns and cues of swimming behaviour. He and others have suggested that swimming can play an important role at these smaller scales, particularly in vertical displacement of larvae.

When larvae are released in the water column, they may remain within the water parcel that overlies the adult habitat, or they may be introduced into a different water layer and get advected by currents (e.g., Pedrotti and Fenaux 1992). Larvae that are advected to the open ocean may be returned to adult habitats in distinct pulses within water parcels that are upwelled or associated with internal bores (Shanks and Wright 1987; Pineda 1994). The boundaries of water parcels usually are delineated by physical and (or) biological discontinuities, such as pycnoclines and layers of chlorophyll maxima, and they may occur at fronts with high shear and pronounced turbulence. To remain near or to be returned to the adult habitat, larvae may have to avoid crossing water parcels, and thus may aggregate at these boundaries. These aggregations could result from a behavioural response to the physical or biological features of the boundaries or from the passive accumulation of organisms with a different specific gravity than the surrounding medium.

Although meroplanktonic larvae descend to the benthos near the end of their larval existence, the relative importance of hydrodynamics and behaviour in larval supply to the substratum has been studied extensively and is well understood, particularly at small spatial scales (for reviews, see Butman 1987; Snelgrove and Butman 1994). While in the plankton, larvae generally had been considered to behave as passive tracers because most studies examined their horizontal displacement at large spatial scales and in strong flow regimes. Over the past decade, however, recognition of the potential importance of swimming behaviour in larval displacement in the water column has triggered an expanding body of research. At this early stage, I believe that an evaluation of the advances and limitations of the existing evidence can be beneficial in directing ongoing and future research on this topic.

I provide a perspective on the relative importance of hydrodynamics (particularly turbulent flow) and swimming behaviour in generating distributions of invertebrate larvae around physical (haloclines, thermoclines, bores, and fronts) and biological (layer of chlorophyll maximum and food patches) features in the water column. This perspective is premised by our extensive knowledge of factors influencing larval supply to the benthos. Specifically, it is well established that in the benthic boundary layer, hydrodynamics are primarily responsible for delivery of competent larvae to appropriate settlement sites (Butman 1987). However, once these larvae enter the logarithmic layer or the viscous sublayer (i.e., within centimetres to millimetres above the substratum), they selectively settle in response to physical, chemical, and biological cues associated with the bottom (Mullineaux and Butman 1991). Selective settlement can be effectuated by an increased ability of the larvae to regulate their position in reduced flow speeds (Butman 1987) or by increased retention resulting from the vertical shear within the viscous sublayer (Jonsson et al. 1991). Similar interactions between hydrodynamics and behaviour may be operating at boundaries in the water column, but only if larvae can alter their swimming behaviour in response to the biological and physical structure in their environment and regulate their position in the dominant flow regime. It should be noted, however, that different selective constraints probably operate during the "dispersive" planktonic period of larval life than during the "retentive" period of competence and settlement within the benthic boundary layer. While in the plankton, larvae generally are positively buoyant, negatively geotactic, and positively phototactic, which causes them to swim away from the bottom and towards the sea surface to seek food and escape predation. In contrast, competent larvae become negatively buoyant, positively geotactic, and negatively phototactic, which increases their probability of descent to the benthos.

Where the information on meroplankton is limited, I invoke evidence from studies on holoplankton and fish larvae to propose mechanisms that may be responsible for observed distributional patterns of invertebrate larvae and warrant further study. This indirect evidence should be viewed with caution because some meroplankton are weaker swimmers than holoplankters and larval fish. (For the interested reader, Dower et al. (1997) provided a comprehensive review on behaviour of fish larvae (particularly feeding) in different flows.) I identify deficiencies in our understanding of processes that generate the observed distributions of invertebrate larvae and provide suggestions for future research, both in laboratory and in field settings. In particular, I argue that studies of biological processes (such as larval swimming or feeding) should incorporate detailed measures of physical processes (such as shear or turbulence) to better understand the mechanisms that generate the observed distributional patterns of larvae in the ocean. Because of a perceived inaccessibility to a relatively simple mathematical explanation, accurate quantification of flow is often avoided by biologists despite its paramount importance in these studies. Therefore, I append a basic mathematical treatment of the quantification of turbulent diffusion, which I consider comprehensible to the interested biologist.

Larval distribution around physical features of the water column

Spatial distributional patterns of invertebrate larvae in relation to physical features in the water column, such as haloclines, thermoclines, and fronts, have been observed both in descriptive studies in the field and in experimental studies in the laboratory. In the field, larval aggregations at or immediately above or below haloclines have been recorded for several invertebrate taxa, such as the polychaete *Owenia fusiformis* (Thiébaut et al. 1992) or an assemblage of bivalve veligers (mainly *Mytilus edulis*) (Raby et al. 1994). On Georges Bank, Northwest Atlantic, Tremblay and Sinclair (1990*a*) found that the centre of mass of the distribution of veligers was within or immediately above the pycnocline for the giant scallop *Placopecten magellanicus*. The magnitude of aggregation was positively related to the strength of stratification (Tremblay and Sinclair 1990*a*), but a minimum stratification may be required for aggregation to occur (Tremblay and Sinclair 1990*a*, 1990*b*). Also on Georges Bank, Gallager

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et al. (1996*a*) found aggregations of ophioplutei below a strong thermocline that occurred between fronts. Increased densities of larvae of several invertebrate taxa (e.g., brachyuran and anomuran crabs, polychaetes, and barnacles) have been recorded in surface slicks at convergences resulting from internal waves (Shanks and Wright 1987). Pineda (1994) found increased densities of crab larvae at convergences of warmwater fronts (indicated by sharp increases in water temperature) associated with internal tidal bores that were passing through rather than ahead or behind the fronts. In a more detailed study, Pineda (1999) showed that larval distribution at such fronts varied among species: cyprids of the barnacle *Pollicipes polymerus* aggregated at the front, whereas those of *Chthamalus* had similar abundances at the front as ahead and behind the front; cyphonautes of *Membranipora* were not found at the front, although they were present both ahead and behind the front.

In the laboratory, altered larval distributions in response to the presence of haloclines have been documented for several taxa including echinoplutei (Metaxas and Young 1998*a*), ascidian tadpoles (Vázquez and Young 1996), barnacle nauplii (Harder 1968), littorinid (Harder 1968) and bivalve veligers (Mann et al. 1991), and decapod zoeae (Sulkin and Van Heukelem 1982). The effects of thermoclines on larval vertical distributions have not been demonstrated as consistently across taxa. For example, thermoclines of >5°C had strong effects on the distribution of echinoplutei (Pennington and Emlet 1986), scallop veligers (Gallager et al. 1996*b*), and some crab larvae (McConnaughey and Sulkin 1984) but not on that of others (Sulkin et al. 1983). It should be noted that the strong effects in all of these studies were associated with very sharp pycnoclines (i.e., gradients of several degrees Celsius or practical salinity units (psu) over vertical distances of 1–10 cm) that occur in few habitats in the field. Mann (1988) found that oyster veligers readily crossed a halocline with a salinity gradient similar to the one in their natural habitat.

Larvae may regulate their position around pycnoclines by modifying their swimming behaviour as they approach the discontinuity. They may remain below or within the pycnocline either by alternating periods of upwards swimming with passive sinking, by swimming horizontally, or by arresting swimming completely and thus remaining at a fixed position if they are neutrally buoyant (McConnaughey and Sulkin 1984; Metaxas and Young 1998*a*). Mann et al. (1991) showed that upward swimming speed of bivalve larvae increased with increasing salinity in *Spisula solidissima* and with decreasing salinity in *Rangia cuneata*, but there was no relationship between downward swimming speed and salinity for either species. A positive relationship between swimming activity and salinity also has been documented for crab zoeae (Sulkin 1984; Forward 1989). These results provide a possible behavioural mechanism for the swimming arrest exhibited by some larvae as they approach areas of decreasing salinity.

Larval distribution around biological features of the water column

The distributional patterns of invertebrate larvae in relation to biological features in the water column, such as areas of increased concentration of chlorophyll *a*, have received little attention either in the field or in the laboratory. Scant field evidence suggests that spatial aggregations of invertebrate larvae may coincide with areas of increased concentration of phytoplankton, mainly at or near pycnoclines and fronts. In the Baie de Chaleurs, Québec, Canada, aggregations of bivalve veligers (mainly *Mytilus edulis*) occurred immediately below the pycnocline and the layer of chlorophyll maximum, but only during the day (Raby et al. 1994). Positive correlations of the concentration of chlorophyll *a* with larval distribution at night, as well as with a larval feeding index, suggested that diel vertical migration was related to increased feeding in the subsurface layer. In contrast, Tremblay and Sinclair (1990*a*) concluded that the centre of mass of the distribution of chlorophyll *a* did not coincide with that of scallop veligers on Georges Bank. However, the vertical distributions in that study show the greatest concentration of larvae at or immediately below the depth of the maximum concentration of chlorophyll *a* under stratified conditions. Also, on Georges Bank, Gallager et al. (1996*a*) reported coincidence of high densities of ophioplutei and of diatom colonies of *Chaetoceros socialis* on a frontal region.

In the laboratory, few studies have examined the effect of biological structure of the water column on the distribution of meroplankton. Metaxas and Young (1998*b*, 1998*c*) found that echinoplutei aggregated (apparently by choice) either in food patches placed in the middle of a water column or immediately below the patches, depending on algal density in the patch. In experimental microcosms, Gallager et al. (1996*b*) and Pearce et al. (1996, 1998) found that placing a high concentration of food in the bottom water layer did not override the inhibitive effect of the presence of a thermocline on downward swimming of scallop veligers.

Modifications in swimming behaviour that may effect the observed distributions could be manifested through changes in swimming characteristics when larvae are near or in a food patch. While no direct measures of such changes have been published for meroplankton, studies on the response of holoplankton to food patchiness suggest that larvae may also be capable of adjusting their swimming behaviour in response to increased concentrations of food. For holoplankton, certain aspects of swimming and feeding behaviour (e.g., frequency of feeding bouts and jumps, and horizontal displacement) were altered, presumably to allow the animals to remain within the patch (Price 1989; Tiselius 1992). Changes in swimming may arise either as a direct result of physical disruption of swimming (e.g., through particle interference with ciliary activity) or by a behavioural response prompted by mechanoreception of particles by cilia or setae. For example, Molares et al. (1994) alluded to brief arrests in swimming (few seconds) to remove food particles from their setae by nauplii of the barnacle *Pollicipes cornucopia*. A behavioural response should be evoked by the potential benefit of increased consumption in areas of enhanced food concentration. Hansen et al. (1991) showed that veligers of the gastropod *Philine aperta* reduced their swimming speed by 40% and increased the radius of the swimming helix in increased concentrations of particles, resulting in enhanced feeding rate. Similarly, holoplankters are known to modify swimming behaviour and patterns of vertical mi-

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gration to enhance feeding rates (e.g., Huntley and Brooks 1982; van Duren and Videler 1995). Detailed descriptions of changes in the swimming behaviour of invertebrate larvae in response to the presence of food are still lacking. Such descriptions would increase our understanding of the role of behaviour in generating aggregations in response to the biological characteristics of boundaries in the water column.

Relative roles of swimming behaviour and hydrodynamics

Larval displacement in the water column results from the interactive effects of hydrodynamics (here termed "flow") and larval swimming (here termed "behaviour"). The flow components relevant to larval displacement are horizontal advection, which results in directed displacement, and turbulent diffusion, which is assumed to result in random displacement and spreading of a group of particles. The slow swimming speeds of invertebrate larvae preclude a behavioural effect on along-stream larval displacement at high flow speeds. However, horizontal flow velocities decrease to near zero at discontinuities such as pycnoclines, possibly allowing larvae to control their displacement as they approach them. Alternatively, larvae may become entrained into a new water layer by the increased turbulence at the mixing interface.

Under natural flow regimes in the field, the role of swimming behaviour in larval displacement relative to physical and biological discontinuities in the water column is unclear. Tremblay and Sinclair (1990*a*) found no evidence that swimming behaviour affected the aggregation of scallop larvae around a thermocline on Georges Bank. Mann (1988) suggested that solely passive dispersal determined the distribution of bivalve larvae relative to a spatially complex frontal system in the James River, Virginia, U.S.A. Similarly, Gallager et al. (1996*a*) proposed that aggregations of both ophioplutei and diatom colonies near the thermocline on Georges Bank could have resulted from the same physical process, thus indirectly discounting a behavioural mechanism. In contrast, Pineda (1999) suggested that species-specific patterns of aggregation at warmwater fronts might be explained by differences in larval swimming ability. He proposed that, unlike barnacle cyprids, the cyphonautes of *Membranipora* did not aggregate at the front because they are weaker swimmers and could not outswim the downward flows at the convergences that carried them away from the front. Similarly, Shanks et al. (2000) found a concentration of strong-swimming larvae (sergestid shrimps, spionid polychaetes, and crabs) near the seaward surface of a propagating upwelling front, presumably because they can maintain their position relative to the downward flow at the convergence. In the laboratory, the studies that ascertained the importance of behaviour in generating larval aggregations around physical and biological discontinuities in the water column were done under "no-flow" conditions (e.g., Metaxas and Young 1998*a*, 1998*b*, 1998*c*). Thus, the relative importance of behaviour in determining larval displacement under different flow regimes remains relatively unexplored.

Swimming behaviour and horizontal advection

At large spatial scales (metres to 100s of kilometres), horizontal advection is the most important factor regulating larval dispersal (for reviews, see Scheltema 1986; Shanks 1995*a*). Larvae may be advected away from the parental habitat either directly offshore (even across the continental shelf) or alongshore for great distances (Roughgarden et al. 1988). At these large spatial scales, larval transport is mainly the result of hydrodynamics with little contribution from swimming behaviour (e.g., Clancy and Cobb 1997). Similarly, retention of slow-swimming larvae (such as veligers and echinoplutei) within enclosed embayments has been considered passive and attributed to horizontal hydrodynamics (Cameron and Rumrill 1982; Tremblay and Sinclair 1990*b*). Several mathematical models have predicted larval dispersal and subsequent recruitment using advection by currents as the only process of larval transport (e.g., Jackson and Strathmann 1981; Alexander and Roughgarden 1996). However, a model by Katz et al. (1994) could only predict the observed spatial and temporal patterns in recruitment of American lobster (*Homarus americanus*) in southern New England, U.S.A., when onshore transport of postlarvae by the dominant currents was coupled with continuous larval swimming. Using another physical circulation model, Tremblay et al. (1994) showed that the transport of larvae of sea scallops on Georges Bank was determined mainly by the circulation pattern, although larval vertical position in the water column (determined by larval swimming) also had an effect on the location of settlement.

At small spatial scales (centimetres to metres), little is known about the interactive effects of horizontal advection and behaviour on larval displacement in the water column. Luckenbach and Orth (1992) showed that the swimming speed of megalopae of blue crabs decreased with increasing flow speed in a flow tank. These larvae were capable of swimming upstream when flow speed was <4 cm·s^{-1} (and showed bursts in swimming speed as great as 24 cm·s^{-1} over distances of <10 cm) and behaved as passive drifters only when flow speed exceeded 9.3 cm·s^{-1}. These results indicate that fast-swimming larvae may be able to regulate even their horizontal displacement at realistic flow speeds.

The combination of large-scale effects of horizontal advection and small-scale effects of behaviour on larval displacement is best illustrated by the model for dispersal and recruitment of blue crabs in Chesapeake Bay and Delaware Bay, U.S.A. In estuaries with established populations of adult crabs, zoeae are most abundant near the surface during ebb tides, whereas megalopae (a later larval stage) are distributed throughout the water column and are most abundant at flood tides (Epifanio et al. 1984). Zoeae released near the mouth of the estuaries are exported to the open ocean where larval development probably occurs, and the megalopae must find their way back to an estuary to settle (Epifanio 1995). Hydrodynamics are responsible for the retention of exported zoeae and megalopae over the Mid-Atlantic Shelf (even near the parental estuary) and for the reintroduction of megalopae into the estuaries (Johnson and Hess 1990; Little and Epifanio 1991; Epifanio 1995). Zoeae may be able to influence their probability of retention or dispersal by exhibiting strong vertical migration to remain near the surface (e.g., Sulkin and Van Heukelem 1982; Sulkin 1984). Also, megalopae may remain near suitable areas for settlement once inside the estuary by using well-timed verti-

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cal migration to take advantage of the predominant flows (Little and Epifanio 1991; Epifanio 1995).

Swimming behaviour in turbulent flows

In the ocean, pronounced turbulence resulting from velocity shear usually occurs at boundaries of water parcels, such as fronts. Wind-generated turbulence may erode the bottom of the mixed layer but remains confined within that layer and dissipates at pycnoclines (Pond and Pickard 1983; Gargett 1989). Turbulent kinetic energy (TKE) is transferred from the local mean flow by large-scale turbulent eddies to progressively smaller eddies until, at the smallest scales of motion, the energy is ultimately dissipated into heat by viscosity. The smallest scale of fluid motion that can exist is estimated by the Kolmogorov microscale (Tennekes and Lumley 1972), and typical Kolmogorov length scales (η) are 100 μm to 1 cm (Hill et al. 1992; Kiørboe and Saiz 1995) (see "Quantification of turbulent diffusion" in the Appendix for equations that describe Kolmogorov scales).

An interactive effect between swimming behaviour and turbulent flow on larval displacement depends on the overlap of the length scales of the flow and the organism of interest (Denman and Gargett 1995). For each eddy size l, only the displacement of larvae with size on the order of l will equal the additive effect of the velocity fluctuation of these turbulent eddies and the swimming velocity of the larvae. The displacement of larger individuals is independent of eddies of this particular size (although not of turbulent motion altogether). Individuals smaller than l will be transported within these eddies and, if l is equal to η, may experience a viscous medium. In the ocean, measured values of the dissipation rate of TKE, ε (see Appendix), range from 10^{-5} to 10^{-14} $m^2 \cdot s^{-3}$ (e.g., Lueck et al. 1983; Haury et al. 1990), and viscosity of seawater, ν, is 10^{-6} $m^2 \cdot s^{-1}$. The length scale of η is 100s of micrometres to 10s of centimetres (see eq. A6 in the Appendix for calculation) and coincides with the length scale of individual invertebrate larvae (100s of micrometres to 10s of millimetres). Thus, the Kolmogorov length scale is the relevant scale at which to examine the interactive effects of turbulent motion and swimming behaviour on the displacement of invertebrate larvae. Although specific swimming responses to turbulence are difficult to predict, larval behaviour probably becomes progressively less important in determining larval displacement with increasing intensity of turbulence. There probably will be a threshold of intensity at which larvae will act like inert particles (i.e., the behavioural component will play no role in their displacement), and this threshold will be higher for stronger swimming larvae (e.g., barnacle nauplii and crab zoeae) than weakly swimming ones (e.g., echinoplutei and bivalve veligers).

The effect of turbulence in the water column on the swimming behaviour of invertebrate larvae is largely unknown (Young 1995). It is doubtful that larvae can control their horizontal and vertical position in the water column with respect to large-scale eddies, but they probably are able to do so in response to small-scale turbulence. The only published study on the effect of turbulence in the water column on invertebrate larvae showed that megalopae of the blue crab *Callinectes sapidus* ascended in the water column in a small flow tank when TKE increased and descended when it decreased (Welch et al. 1999). Although the larvae responded to changes and not to absolute levels of TKE, the authors also suggested that there might be a threshold absolute value that cues the swimming response.

Based on studies done on holoplankton, the distribution of larvae of marine invertebrates relative to boundaries in the water column may result from modifications in swimming behaviour in turbulent flows. For calanoid copepods and larval fish, swimming behaviour may be altered in the presence of small-scale turbulence, perhaps to compensate for perceived changes in the physical and biological environment. In calanoid copepods, characteristics of swimming behaviour that can differ between turbulent and nonturbulent conditions include jumping velocity, the number of jumping and feeding bouts, and the percentage of time spent slow and fast swimming (Costello et al. 1990; Saiz 1994). Similarly, for fish larvae, small-scale turbulence can affect characteristics such as the amount of time spent swimming (MacKenzie and Kiørboe 1995). Invertebrate larvae may be induced to alter their swimming behaviour at a lower threshold of turbulent velocity (and (or) at slightly smaller eddy sizes) than copepods and fish larvae because they are weaker swimmers. Thus, invertebrate larvae may require being nearer a particular boundary, and thus in areas of lower shear, than copepods and fish larvae before they can respond to its physical and biological characteristics. Experimental evidence and numerical models for calanoid copepods and fish larvae showed that encounter rates between predators and prey increased with increasing small-scale turbulence (Rothschild and Osborn 1988; Saiz 1994) (or showed a dome-shaped response; MacKenzie et al. 1994). Similar modifications in swimming behaviour of invertebrate larvae in areas of increased small-scale turbulence potentially will be dictated by two opposing constraints: larvae may aggregate in these areas to increase encounter rate with food particles or they may avoid such areas to decrease encounter rates with their predators.

Numerical models, particularly random walk models, are becoming increasingly popular in predicting the movement of planktonic organisms (as particles) in a turbulent water column (Yamazaki 1993; Visser 1997; Porch 1998). The simple random walk is a langrangian model that follows tracks of randomly moving particles in space and time and calculates the probability distribution of their displacement (Csanady 1973; Okubo 1980). The change in the concentration of particles at a specified location over time $\left(\frac{\partial S}{\partial t}\right)$, resulting from advection and diffusion, can be estimated by multiplying the probability that an individual particle will reach that location over that time $\left(\frac{\partial p}{\partial t}\right)$ with the total number of released particles (see "Description of the random walk model" in the Appendix for mathematical description). Yamazaki (1993) proposed two langrangian models to describe displacement of a swimming organism. One of the models (the aggregating random walk model) treats swimming patterns as if the organism is a particle with Brownian motion in a field of external force (gravity). In this model, the acceleration of the organism is equal to the sum of the viscous force on the speed of the organism, a random walk component resulting from turbulence, and the gravitational force. In an alternative model (the nonparametric probability

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density function patch model), Yamazaki (1993) proposed to quantify the attractive force of plankton towards the centre of an aggregating patch. The displacement of a particle at each time step is given as the sum of a component for a random walk (the result of turbulence, with values generated from a Gaussian distribution) and a component for a biological attractive force. The attractive force is estimated as

$$W_A = \beta P(x)/dx$$

where $P(x)$ is the instantaneous distribution of particles around a point x and β is a constant directly proportional to an attractive walk toward the centre of the population and a function of the swimming ability of the organism. Visser (1997) cautioned that a diffusive random walk model that incorporates a gradient of diffusivity along the z-axis is more appropriate than a naive random walk model in which diffusivity remains constant over z (neither of these models included a component of biological attractive force). His study was predicated on the fact that in the naïve random walk model, neutrally buoyant particles (or other passive tracers) eventually begin to accumulate in regions of low diffusivity. Although appealing as a mechanistic explanation for the aggregation of particles such as larvae, this is an incorrect result generated by a model that must apply to all types of particles. If the particles being considered were salt ions, this result would imply that salinity would always increase in areas of low turbulence, which is not the case. Using computer simulations, Visser (1997) demonstrated that including a nonrandom term that describes the gradient in diffusivity alleviates this limitation.

The use of numerical models has provided some indications of the potential importance of swimming behaviour in plankton displacement under turbulent regimes. Yamazaki and Kamykowski (1991) suggested that the ciliate *Mesodinium rubrum* could maintain patterns of diel vertical migration in a thoroughly mixed water column at wind speeds of 5–10 $m \cdot s^{-1}$. Yamazaki and Squires (1996) showed that the swimming velocity of calanoid copepods is slightly greater than the turbulent velocity that corresponds to values of ε observed in the field, and thus the displacement of these organisms potentially may be independent of turbulent motion. Porch (1998) suggested that random swimming of larvae does not contribute significantly to their horizontal diffusion on large spatial and temporal scales; however, swimming may be important in their vertical diffusion because vertical turbulence is much weaker than horizontal turbulence. Swimming may only increase larval horizontal diffusion significantly in habitats of relatively low turbulence (e.g., small isolated bodies of water such as bays), where the decorrelation time scale of turbulence (i.e., the time period over which the end fluid velocity is no longer correlated with initial fluid velocity) is on the order of minutes.

Using a random walk model that combined the effects of swimming and turbulent diffusion, Davis et al. (1991) showed that predators accumulated in areas of increased food concentration and that the magnitude of accumulation depended on swimming characteristics such as the rates of stopping, starting, and swimming. The authors concluded that population growth of the predator increased with increasing variability in swimming, an indication of the organism's ability to move in and out of patches.

Numerical models can be used to increase our understanding of the interactive effects of turbulent flow and swimming behaviour on the distribution of invertebrate larvae. Different parameters can be manipulated, such as the level of turbulence to reflect a particular habitat or a swimming characteristic hypothesized to be modified in the presence of turbulent flow (e.g., changes in frequency of turning or in swimming speed as reflected in the trajectory of a particle in a random walk model). Predictions of the effects of these different parameters on the distribution of larvae can then be generated, which in turn can be tested in the field. Also, the experimental information collected on taxa other than invertebrate larvae, such as calanoid copepods and fish larvae, can be used to parameterize the numerical models. These relatively realistic models can then be used to generate predictions on invertebrate larvae from the same habitat.

Perspectives on past and future research

There is strong evidence that physical and biological discontinuities shape vertical distributions of invertebrate larvae in the water column. Some experimental evidence has suggested that larval behaviour potentially plays an important role in the generation of such patterns. However, the mechanism by which swimming behaviour of individuals can modify the distribution of a population, although implied, has not been described quantitatively. Also, both the physical regimes and the spatial scales at which swimming behaviour can influence the generation of distributional patterns need to be defined. Presently, there are several limitations in the quantification of swimming behaviour and of relevant flow regimes that need to be addressed.

Quantification of larval behaviour

In the field, quantification of flow regimes is becoming increasingly more sophisticated, but that of larval behaviour remains fraught with logistical difficulties. One hindrance is that the presence of larvae in the water column is unpredictable. Although the general timing of larval release is known for a large number of taxa, development times in nature (and thus planktonic period) can be quite variable (for a review, see Strathmann 1987). For free spawners, information on frequency of spawning, fertilization rates, and hence larval production at any one time is generally lacking. We are only just beginning to understand the patterns in larval dispersal that may result in great local dilution of recently released larvae. Field studies have shown that larval density in the water column is generally on the order of <10 to 100s·m^{-3}, making detection and quantification of spatial and temporal patterns difficult.

Because of their low density, spatial and temporal unpredictability, and small size, long-term tracking of naturally occurring or released larvae has met with limited success. Long-term tracking requires that a large pool of larvae can be identified, followed, and sampled repeatedly over periods of weeks and distances of 100s of kilometres. A variety of markers (e.g., stains, radioactive labels, and genetic markers) have been tried for invertebrate larvae (for a review, see Levin 1990), but most recent research has focused on trace

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elements. Levin et al. (1993) labeled larvae with rare-earth elements (europium, lutetium, and samarium) because their background concentrations in estuarine plankton are extremely low, they can be easily applied by exposing larvae in solutions of the desired element, and they are environmentally safe. However, the labels were retained in larvae for periods of only hours to days, they induced mortality in some genera (e.g., the clam *Mercenaria mercenaria*), and their measurement was quite costly. Recently, selenium has been proposed as a more suitable larval label because larvae assimilate it readily through feeding on ^{35}Se-labeled phytoplankton, and they retain it at detectable concentrations for weeks (Anastasia et al. 1998). At small temporal (seconds to hours) and spatial (metres to 10s of metres) scales, it is possible to manually track large individual larvae (e.g., crab megalopae and ascidian tadpoles) by snorkeling or scuba diving (Bingham and Young 1991; Shanks 1995*b*).

Another impediment to quantifying larval behaviour in the field is that observational tools for visualization at scales of millimetres are limited and expensive. Among the most sophisticated tools available is the video plankton recorder (VPR), an underwater-towed microscope designed to minimize disturbance of the sampled volume (Davis et al. 1992). The VPR consists of four video cameras with magnifying optics for sampling volumes of 0.9–640 mL, with a resolution of 10 µm. Gallager et al. (1996*a*) used the VPR to attain images of individual holoplankters (calanoid copepods) and meroplankters (ophioplutei) collected near fronts on Georges Bank. Unfortunately, the state-of-the-art technology of the VPR makes it prohibitively expensive, and its wide use is unlikely at present. Recently, Tiselius (1998) presented a similar but cheaper optical sampler based on a single CCD video camera. The volume sampled with this device was 0.42 mL, and Tiselius used it to identify calanoid copepodites to species. Either of these optical systems could provide some information on the swimming behaviour of individuals in areas, such as boundaries in the water column, selected for particular physical and biological characteristics. Using a eulerian approach, spatial or temporal changes in the distribution of particles relative to a feature in the water column, such as a pycnocline, can be recorded by fixing the position of the optical system. Comparisons of the distributions of larvae and nonmotile particles, such as phytoplankton cells, can provide indirect measures of the effects of swimming and flow. Using a langrangian approach, a feature can be tracked and a video record of particles obtained by allowing the optical system to drift (or towing it) at the speed of the dominant flow. Differences between tracks of individual larvae and those of nonmotile particles can provide a direct description of swimming characteristics. At small spatial and temporal scales, tracking of larvae released into the water column also may be possible.

Given the limitations of field studies, controlled experiments in the laboratory provide a more effective means of directly observing larval behaviour in response to physical and biological parameters within the natural range. Factors that can be studied or manipulated include velocity of laminar flow (in a flow tank), turbulent velocity (in an oscillating grid system), characteristics of food patchiness (e.g., algal density in a patch and patch density in the water column), and larval swimming ability. This approach can provide a first estimate of the potential role of behavioural responses of larvae to their environment, leading to hypotheses that can be tested directly in the habitat of interest.

Behavioural modifications in response to physical and biological features of the environment, as reflected in specific swimming characteristics, have not been described quantitatively for meroplanktonic larvae. More accurate measurements of swimming speeds and trajectories are needed if we are to assess the importance of swimming behaviour in larval dispersal. Swimming speeds of larvae have been measured mainly for bivalve larvae (e.g., Mann and Wolf 1983; Mann et al. 1991), but some measures also exist for annelids, barnacles, echinoderms, crabs, and ascidians (Chia et al. 1984). Speeds range from 0.1–0.4 mm·s^{-1} for the slow-swimming larvae of echinoderms to 3–7 mm·s^{-1} for powerfully swimming crab zoeae (e.g., Chia et al. 1984). Swimming trajectories have been described only for bivalve trochophores (Mann and Wolf 1983; Jonsson et al. 1991) and ascidian tadpoles (Svane and Young 1989). However, measures of swimming characteristics of calanoid copepods (van Duren and Videler 1995) can be extended to invertebrate larvae. These include swimming speed, proportion of total time spent swimming, mean direction of travel, angular deviation (i.e., standard deviation of the distribution of angles in a trajectory, a measure of turning behaviour), net to gross displacement rate (i.e., ratio of linear distance between the beginning and end of a swimming path to the total distance traveled, also a measure of turning behaviour), and mean orientation of individuals.

Generation and quantification of turbulence

There are several directions in which we can proceed to increase our understanding of the roles of hydrodynamics and swimming behaviour in larval displacement in the water column. Unchartered research areas of particular interest include the examination of the relative roles of flow and swimming at spatial scales relevant to behaviour (on the order of micrometres to metres) and of differences in the relative importance of these two factors among larvae of different swimming abilities. Studies that examine larval displacement in laminar flow certainly are necessary; however, their outcome can be predicted because of the additivity of the effects of laminar flow velocity and larval swimming velocity. Addressing these two questions in turbulent flows is a more challenging research direction. Two major challenges at present are quantification of turbulent flow in the field and laboratory and generation of turbulent regimes in the laboratory that are representative of those in the field.

Quantification of turbulent flows can provide a major challenge relative to that of laminar flows, particularly to a biologist. Laminar flow regimes are well defined and deterministic, making their mathematical description relatively uncomplicated. In contrast, turbulence is a random flow motion, in which instantaneous flow speed (u) fluctuates randomly (by u') around a mean value ($\bar{u}$). In turbulent flow, the relative paths of two particles may remain parallel, converge, or completely diverge under the same regime of turbulence. Consequently, numerical modelers generate complex mathematical descriptions of turbulent flow regimes that are not easily understood by biologists. The most easily obtained and frequently used measure of turbulence is the rate of dis-

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sipation of TKE, ε. To calculate ε, two parameters must be measured: the standard deviation of the mean fluctuating velocity ($(\overline{u'^2})^{1/2}$), also known as the fluctuating root mean square velocity, and a factor (ℓ) that scales the largest eddy size to the width of flow (see eqs. A2–A7 in the Appendix for mathematical derivations).

Several methods have been used to generate turbulence in the laboratory. The simplest include shaking, stirring, and vibrating of small experimental vessels such as flasks and jars (e.g., Saiz and Alcaraz 1992*b*). Pearce et al. (1998) introduced air bubbles to the bottom of a 117-m^3 mesocosm, generating turbulence as the bubbles rose through the water column. Welch et al. (1999) generated TKE in a flow tank by adding piles of rocks upstream from the working section and by varying flow speed. Although these methods generate a "mixed" water column, the turbulence regime is difficult to quantify and reproduce. These limitations can be overcome partly by using a linearly oscillating grid of bars (Saiz and Alcaraz 1992*a*; MacKenzie and Kiørboe 1995). The grid may be oriented horizontally (covering the entire cross-sectional area of the experimental vessel) and oscillate vertically (e.g., MacKenzie and Kiørboe 1995), or it may be oriented vertically (at one corner of the vessel) and oscillate horizontally (e.g., Saiz and Alcaraz 1992*a*). The characteristics of the produced turbulence can be manipulated by adjusting the parameters of the grid oscillation: the spacing (M) and bar thickness of the grid mesh, amplitude of oscillation, and frequency of oscillation. The generated turbulence is reproducible, near homogeneous (particularly in the horizontal plane, but also in the vertical), and near isotropic at a distance as small as $3M$ from the grid (de Silva and Fernando 1994) This type of turbulence field has been well characterized in a number of studies (Laws and Livesey 1978; Brumley and Jirka 1987).

Although realistic ranges of ε may be generated in the laboratory, reproduction of the Reynolds numbers (Re) at which the Kolmogorov calculations (eq. A6 in the Appendix) are valid is difficult. The Re (a dimensionless ratio of the inertial to viscous forces that operate in a particular flow regime) is the pivotal scaling parameter for physical processes occurring at a range of spatial or temporal scales. It depends on the length and velocity scales of the flow regime and on the kinematic viscosity of the fluid. Two different systems with equal Re, such as an experimental flow tank in the laboratory and a particular habitat that it is designed to reproduce, are assumed to have the same flow characteristics. Because the size of experimental tanks (and thus grid dimensions) is constrained, the length scales of flow are much smaller in the laboratory than in the ocean, and therefore, extrapolations must be done with caution. This limitation will not impede the generation of realistic measures at scales relevant to swimming behaviour (millimetres to centimetres) but will constrain extrapolations at scales relevant to distributional patterns of populations (100s of metres to kilometres).

Identification of forcings on the biological spatial structure

Unconfounding the physical and biological forcings that operate on the generation of larval aggregations in the water column remains a major challenge. Spectral analysis is a technique that can be used to determine whether the statistical spatial (or temporal) structure of a biological variable (e.g., larval abundance) matches that of turbulent motion. This analysis is based on the tendency of nonlinear biological systems to show periodicity, which may reflect periodicity in the input of external energy (for a review, see Platt and Denman 1975). With Fourier analysis, a data series of the biological variable can be decomposed into a sum of sine and cosine functions of different spatial (e.g., millimetres to kilometres) or temporal (e.g., seconds to hours) frequencies. A spectrum is then generated by partitioning the total variance in the series into contributions from different wavelengths that correspond to the different frequencies. A spectrum of TKE can be generated by calculating the spectral density of turbulent energy, $E(k)$, for eddies of different wave numbers k within the inertial subrange (see "Quantification of turbulent diffusion" in the Appendix for calculations). The measure required to calculate $E(k)$ is the fluctuating mean square velocity ($\overline{u'^2}$). Comparisons between spectra of different variables can be drawn, using cross-spectral techniques that estimate covariance of the variables in each frequency, to infer causal relationships between variables (Platt and Denman 1975). For example, a similarity in the shapes of the biological spectrum and the turbulent energy spectrum implies that the structure of the biological parameter is controlled primarily by turbulence (Okubo 1980). If factors other than (or in addition to) turbulent diffusion regulate the spatial structure of the biological variable, the biological spectrum will be flatter than (or peak at a frequency different from) that of turbulent energy.

Spectral analysis has been used to explain patchiness in the concentration of chlorophyll (e.g., Denman et al. 1977) and zooplankton (e.g., Mackas and Boyd 1979). Powell and Okubo (1994) also used power spectral analysis in a modeling study to examine the relative effects of biological interactions and turbulent diffusion on the spatial structure of a population. For the physical model, they incorporated in the Navier–Stokes equation a force that generates turbulent diffusion. The biological model was composed of terms for diffusion, population dynamics, and environmental forcing. Using the two models, they generated and compared power spectra of the two variables. At small spatial scales (i.e., in the inertial subrange), the spatial structure of plankton was similar to that of the turbulence field. At large scales, plankton was less patchy than the turbulence field, indicating that its spatial structure was also influenced by biological interactions.

Conclusions

In the field, larvae of marine benthic invertebrates aggregate at physical and biological discontinuities in the water column, such as pycnoclines, fronts, and zones of high concentration of chlorophyll, which often are associated with boundaries of water parcels. In the absence of flow in the laboratory, similar aggregations have been recorded, indicating a potentially significant role of swimming behaviour in generating these distributions. The logical extension of these studies is to examine the relative importance of behaviour in different flow regimes. One of the most intriguing questions is whether meroplanktonic larvae (like holoplankton and fish

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larvae) have the swimming ability to regulate their position in turbulent flows, which often dominate near boundaries in the water column. If so, larval behaviour may be at least partially responsible for the observed patterns in the distribution of meroplankton at density discontinuities. The relative importance of swimming and turbulent flow in larval displacement in the water column has been examined only in one experimental study in the laboratory and in a few studies using numerical models. Clearly, our understanding of the regulation of larval distributions at small spatial scales (millimetres to metres) is rudimentary.

This emerging area of research is both promising and exciting, but there are empirical deficiencies and technological constraints that must be overcome to advance our understanding. In particular, studies that examine larval swimming in flow must rigorously quantify behavioural modifications and flow characteristics at appropriate scales. In the field, observations of larval behaviour are constrained by the unpredictable presence of larvae in the water column, the limited success in tracking larvae, and the lack of appropriate observational tools at scales of millimetres. In the laboratory, where quantification of larval behaviour is more tractable, the main challenge is the generation of flow regimes that are representative of those in the field. If the relative importance of larval behaviour can be measured in the laboratory under a range of realistic natural conditions, hypotheses can then be generated about its potential role in a particular habitat. These hypotheses can be tested directly in the field once appropriate tools become available.

Some components of the planktonic stage of marine invertebrates are becoming increasingly better understood. For example, it is well established that larval dispersal at large spatial scales is regulated mainly by hydrodynamics and that larval settlement is affected by various factors, such as hydrodynamics, availability of suitable substrate, and behavioural responses of larvae to chemical and biological cues. However, the ability of larvae to regulate their position in the water column at small spatial scales remains largely unknown. A well-designed research approach that integrates the study of physical and biological processes will enable us to illuminate yet another corner of the black box of larval life.

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Appendix

Quantification of turbulent diffusion

Unlike other physical processes that operate on large spatial scales, such as advection by ocean currents, the understanding and quantification of turbulence both in the field and in the laboratory still present a great challenge (Gargett 1989; Denman and Gargett 1995). One of the main difficulties is the choice of an appropriate mathematical model that describes accurately turbulent diffusion (i.e., random motion generated by turbulence). Fick's law of diffusion states that the amount of transport of matter in the x direction across a unit area per unit time (or flux, J_x) is proportional to the gradient in concentration of matter. This law is described by the equation

$$\text{(A1)} \quad \frac{\partial C}{\partial t} = -\frac{\partial J_x}{\partial x} \frac{\partial}{\partial x}\left(D\frac{\partial C}{\partial x}\right)$$

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where C is the concentration of matter and D is the coefficient of diffusion (or diffusivity) (Okubo 1980). This equation is only applicable to diffusions for which the length and time scales of motion are much smaller than the length and time scales of observation (e.g., molecular diffusion). However, because in turbulent diffusion the order of magnitude of the typical length and time scales of motion and of observation is similar, a modification of this equation is required (Batchelor 1960; Csanady 1973; Okubo 1980).

Based on the principle of conservation of mass, the flux of particles in the x direction (J_x) in a fluid with laminar flow and an instantaneous horizontal velocity $u(x,t)$ is equal to the sum of the fluxes generated by u and by molecular diffusion and can be described by the equation

$$(A2) \quad J_x = uS - D\frac{\partial S}{\partial x}$$

where S is the concentration of particles. For an infinitesimal volume of fluid around some point x, the equation of diffusion of an instantaneous concentration of particles $S(x,t)$ from x at time t is given by

$$(A3) \quad \frac{\partial S}{\partial t} = -\frac{\partial J_x}{\partial x} = -\frac{\partial}{\partial x}(uS) + \frac{\partial}{\partial x}\left(\frac{\partial S}{\partial x}\right).$$

Because turbulence is a random motion, the motion of a small particle in a turbulent fluid is also considered random (Okubo 1980). Thus, at any time t, S, and u also fluctuate randomly from the statistical average ($\bar{S}$ and $\bar{u}$, respectively) by a certain amount (S' and u', respectively), so that $S = \bar{S} + S'$ and $u = \bar{u} + u'$. If we substitute these values into eq. A3, we obtain

$$(A4) \quad \frac{\partial \bar{S}}{\partial t} = -\frac{\partial}{\partial x}(\bar{u}\bar{S}) + \frac{\partial}{\partial x}(-\overline{u'S'}) + \frac{\partial}{\partial x}\left(D\frac{\partial \bar{S}}{\partial x}\right).$$

In eq. A4, the change in average concentration of particles over time is equal to the sum of net transport by advection (mean velocity), the net transport by turbulence (turbulent diffusion), and molecular diffusion. The diffusivity by turbulence K in the x direction is referred to as eddy diffusivity and can be obtained from (Okubo 1980)

$$(A5) \quad \overline{u'S'} = -K\frac{\partial \bar{S}}{\partial x}.$$

Using a scaling argument, $K \sim uL$ (Tennekes and Lumley 1972). All of the presented one-dimension equations can be easily extrapolated to three dimensions (see Csanady 1973).

The measure used to quantify the turbulence regime in the field and in the laboratory is ε, the rate of dissipation of turbulent kinetic energy (TKE) per unit mass. This dissipation rate along with the kinematic viscosity of seawater ν define the Kolmogorov length scale η in the relationship

$$(A6) \quad \eta = \left(\frac{\nu^3}{\varepsilon}\right)^{1/4}.$$

(The Kolmogorov time and velocity scales are given by $\tau = \left(\frac{\nu}{\varepsilon}\right)^{1/2}$ and $\upsilon = (\nu\varepsilon)^{1/4}$, respectively.)

The dynamics of turbulence imply that energy must be transferred from the largest eddies (which govern the exchange of kinetic energy from mean flow to turbulence) to the smallest eddies (which govern dissipation of TKE through viscous forces) (Tennekes and Lumley 1972). Because energy transfer is dictated by the energy (U^2) and time (U/L) scales of the large eddies, the dissipation rate of TKE can be estimated as

$$(A7) \quad \varepsilon = \frac{A}{\ell}\left[(\overline{u'^2})^{1/2}\right]^3$$

where A is a constant assumed to be of order 1 (Tennekes and Lumley 1972; Hill et al. 1992; Saiz 1994), $(\overline{u'^2})^{1/2}$ is the fluctuating root mean square velocity and is equal to the standard deviation of the mean fluctuating velocity u', and ℓ is the integral length scale that represents the size of the largest eddies, assumed to be equal to the width of flow (Tennekes and Lumley 1972). The integral length scale is assumed to be proportional to the size of the larger eddies because they contribute more to the transfer of momentum than small eddies. Two implications are that energy is extracted from the mean flow at length scales equal to ℓ and that the rate of dissipation of TKE can be estimated solely from the large eddies and thus is independent of the viscous forces.

In addition to calculating ε, spectral analysis of the flow regime also may be useful because of the wide range of length scales that exist in turbulent flows. The dimensions of the turbulent length scales correspond to the different sizes of eddies and fall between the scale of the flow field and that of the diffusion by viscosity (Tennekes and Lumley 1972; Csanady 1973). It is possible to calculate the average characteristic velocity and thus the TKE per unit mass of eddies of different sizes (Csanady 1973). TKE (T) in a given volume V of fluid with density ρ is given by

$$(A8) \quad T = \frac{1}{2}\rho V\overline{u'^2}$$

and TKE per unit mass (T_1) is given by

$$(A9) \quad T_1 = \frac{K}{\rho V} = \frac{1}{2}\overline{u'^2}.$$

By using eddies of several different sizes, a spectrum of TKE can be estimated for a particular turbulence flow field (i.e., for a range of eddy sizes). Spectra decompose a series of measurements into waves of different periods (for time series) and wavelengths (for spatial data) (Okubo 1980). The mean energy in a particular wave is given by the value of the spectrum at a particular wavelength or frequency. Assuming that eddy size coincides with eddy wavelength (λ), a wave number (k) can be calculated ($k = 2\pi/\lambda$) for each eddy size (Okubo 1980). If $E(k)dk$ is the contribution of wave numbers between k and $k + \Delta k$ to T_1, then

$$(A10) \quad \int_0^\infty E(k)dk = \frac{1}{2}\overline{u'^2}$$

where $E(k)$ is the spectral density of turbulent energy or energy spectrum function (Okubo 1980). The "inertial sub-

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range" is a range of eddies of intermediate size that do not receive energy from the main flow and do not dissipate kinetic energy into heat, but rather transfer TKE from larger to smaller eddies (Tennekes and Lumley 1972; Csanady 1973; Okubo 1980). For this reason, the spectral energy of these eddies varies only with the dissipation rate of energy and the wave number of the eddies as

$$\text{(A11)}\quad E(k) = A\varepsilon^{2/3}k^{-5/3}$$

where A is a constant approximately equal to 1.5 (Tennekes and Lumley 1972; Okubo 1980). These characteristics of eddies in the inertial subrange make the calculation of a spectrum of TKE possible and provide a useful tool.

Description of the random walk model

The random walk model is a numerical model that describes spatial or temporal trajectories of individual particles that are moving randomly. In this model, a particle moves in individual steps, and after each time step, the particle "forgets" its initial velocity. Thus, each step effectively is independent of the previous one. In the simplest case of a random walk in the x direction, $p(x,t)$ can be defined as the probability that a particle released from the origin at $t = 0$ will be at point x by time t. At any time step τ, the particle can move either to the right (with probability α) or to the left (with probability β) from its previous location ($\alpha + \beta = 1$). At some intermediate point $t - \tau$, the particle may be either at $x - \lambda$ and approaching x from the left or at $x + \lambda$ and approaching x from the right. Thus:

$$\text{(A12)}\quad p(x,t) = \alpha p(x - \lambda, t - \tau) + \beta p(x + \lambda, t - \tau).$$

By assuming that λ and τ are small compared with x and t and by using a sequence of computations (see Okubo 1980), the equation of diffusion for the random walk of an individual particle can be derived as

$$\text{(A13)}\quad \frac{\partial p}{\partial t} = -u\frac{\partial p}{\partial x} + D\frac{\partial^2 p}{\partial x^2}.$$

If p is multiplied by the total number of particles that were released, the change of particle concentration over time can be calculated as

$$\text{(A14)}\quad \frac{\partial S}{\partial t} = -u\frac{\partial S}{\partial x} + D\frac{\partial^2 S}{\partial x^2}.$$

(Note that eq. A14 is the same as eq. A3.)

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The Precautionary Approach and risk management: can they increase the probability of successes in fishery management?[1]

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Abstract: Considerable progress has been made in the implementation of the Precautionary Approach to the protection of fish stocks, but applying the Precautionary Approach to the protection of fishing communities lags considerably. The principle of intergenerational equity, one of the main tenets of the Precautionary Approach, and the principle of sustainable utilization both imply that the Precautionary Approach should explicitly incorporate the protection of fishing communities, not only the resources they depend on. Risk assessment aims primarily at evaluating the consequences of various harvest strategies in terms of probabilistic statements about future trends in yields, biomass, and dangers to the stock, while risk management involves finding and implementing management policies, strategies, and tactics that reduce the risk to the communities exploiting them. Not all fishery management approaches deal equally well with risk, with some compounding rather than reducing risk. Portfolio management, whereby fishing enterprises have the ability to choose among a diverse portfolio of harvestable resources, would mitigate against the risk of fluctuations in the abundance, availability, or price of individual species. Although much remains to be achieved in better assessing risk, fishery management agencies should immediately implement risk management.

Résumé : Des progrès considérables ont été réalisés dans la mise en œuvre de l'Approche de Précaution pour la protection des stocks de poissons, mais son application à la protection des communautés de pêche traîne considérablement. Le principe d'équité entre les génération, un des fondements de l'Approche de Précaution, et le principe d'utilisation soutenue impliquent tous les deux que l'Approche de Précaution doive incorporer de manière explicite la protection des communautés de pêche, pas seulement les ressources dont elles dépendent. Les évaluations de risque visent principalement à estimer les conséquences de diverses stratégies d'exploitation en terme de probabilité de l'évolution future des rendements, de la biomasse, et des dangers pour le stock. La gestion du risque, d'autre part, consiste à trouver et à mettre en œuvre des politiques, stratégies, et tactiques qui réduisent le risque pour les communautés qui exploitent les ressources halieutiques. Les approches de gestion des pêches ne sont pas toutes équivalentes en terme de gestion du risque, certaines l'augmentant même plutôt que le diminuer. La gestion par portefeuille, grâce à laquelle les entreprises de pêche auraient la possibilité de choisir à même un portefeuille diversifié de ressources, atténuerait le risque qu'entraînent les fluctuations d'abondance, de disponibilité et du prix de l'une ou l'autre espèce. Bien qu'il reste beaucoup à faire pour mieux évaluer le risque, les agences de gestion des pêches devraient immédiatement mettre en œuvre la gestion du risque.

Introduction

The 1990s have seen an increased awareness of the difficulties of fishery management. While fishery collapses had happened before, most notably for herring on Georges Bank, in the North Sea, off Iceland, and in the Norwegian Sea in the late 1960s and mid-1970s, they were attributed to the fragility of pelagic schooling species, immaturity of fisheries science, and failure to implement recommended management measures. This could not be said of the widely publicized collapse of the Northern cod fishery off Newfoundland in 1992: Canada had a fully developed scientific process, extensive monitoring control and surveillance, and an elaborate fishery management advisory process, and cod was not considered a species particularly sensitive to exploitation. Yet, those substantial human and financial resources did not prevent the collapse of the cod fishery. Other examples include the near collapse of Northeast Arctic cod in the late 1980s and again in the second half of the 1990s, of North Sea herring for a second time in less than 20 years, and the severe declines of traditional groundfish resources off New England. Clearly, the uncertainties in fishery science and the difficulties of implementing management measures, particularly catch controls, are substantially greater than previously believed.

The recognition of those uncertainties and difficulties, combined with a gloomy assessment of the world fishery's scene (FAO 1994), helped reach agreement on several

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international instruments in the 1990s stipulating that the Precautionary Approach should be applied to management of the environment and of fisheries (the Rio Declaration, the Cancun summit, the United Nations (UN) Agreement on Straddling Fish Stocks and Highly Migratory Fish Stocks, the UN Food and Agriculture Organization (FAO) Code of Conduct for Responsible Fisheries, the Treaty of the European Union). Although states have moral, and in some cases legal, obligations to implement the Precautionary Approach, the more compelling reason is because the long-term consequences of the results of human intervention on the environment, be it through removing animals from the oceans or through releasing substances, in the atmosphere or in water, are largely unknown. Indeed, if the results of human intervention on the environment were perfectly known and management measures to prevent negative impacts could be perfectly implemented without delay, there would be little risk of irreversible damage and the Precautionary Approach would not be needed.

The developments on the international scene listed above were politically led at the highest government echelon. Concurrently, fishery science, accepting that uncertainties were considerably larger than previously believed, and building on technical development in integrated and Bayesian assessment methodologies, was developing more formal methods of risk assessment by calculating and evaluating the probabilistic consequences of various combinations of assessment assumptions, data treatment, and management measures. This was recognition that fishery management is a problem in decision-making under uncertainty (Smith et al. 1993; Rosenberg and Restrepo 1994; Punt and Hilborn 1997) with the decisions to be made pursuing multiple objectives; the formal analysis is therefore complex.

In this paper, we will briefly review progress on the implementation of the Precautionary Approach in some countries and organizations with which we are or have been personally involved. We will argue that applying the Precautionary Approach to the protection of the resources may lead to unnecessary fishery closures causing irreversible damage to fishing communities, thereby making it impossible to meet the objective of intergenerational equity inherent in the Precautionary Approach; therefore, the Precautionary Approach should explicitly include the protection of fishing communities. We will submit that this should be done by explicitly implementing risk management through risk assessment to evaluate and implement management measures that will reduce the risk that fishing communities are exposed to. We will evaluate various management approaches and their implications with respect to risk management, and we will discuss the implementation of risk management.

Implementation of the Precautionary Approach

In this section, we will first provide a description of the Precautionary Approach and we will then review how the definition has been operationalized in some countries and organizations with whom we are or have been personally involved.

Several definitions of the Precautionary Approach exist, with some differing very little from the Precautionary Principle (Garcia 1996). We believe that the definition below, prepared by the FAO expert consultation on the Precautionary Approach to Fisheries Management (FAO 1996, p. 6), summarizes the main points of what the Precautionary Approach means:

> The precautionary approach involves the application of prudent foresight. Taking account of the uncertainties in fisheries systems and the need to take action with incomplete knowledge, it requires, *inter alia*: (*a*) consideration of the needs of future generations and avoidance of changes that are not potentially reversible; (*b*) prior identification of undesirable outcomes and of measures that will avoid them or correct them promptly; (*c*) that any necessary corrective measures are initiated without delay [...]; (*d*) that where the likely impact of resource use is uncertain, priority should be given to conserving the productive capacity of the resource; (*e*) that harvesting and processing capacity should be commensurate with estimated sustainable levels of resource [...]; (*f*) all fishing activities must have prior management authorization and be subject to periodic review; (*g*) an established legal and institutional framework for fisheries management, within which management plans that implement the above points are instituted for each fishery; and (*h*) appropriate placement of burden of proof by adhering to the requirements above.

FAO (1996, p. 7) also suggests that "the standard of proof to be used in decisions regarding authorization of fishing activities should be commensurate with the potential risk to the resource, while also taking into account the expected benefits of the activities."

The implementation of the Precautionary Approach in the fora that we reviewed shares common features, following the template provided by Annex II of the UN Agreement on Straddling Fish Stocks and Highly Migratory Fish Stocks with emphasis on attempting to quantify uncertainties and on defining reference points and preagreed harvest control rules.

Annex II of the UN Agreement calls for two types reference points: "conservation, or limit, reference points and management, or target, reference points" and suggests that "the fishing mortality rate which generates maximum sustainable yield should be regarded as a minimum standard for limit reference points." Having had a long history of unsuccessfully trying to agree on targets with management agencies, the International Council for the Exploration of the Sea (ICES), who took an early lead on implementing the Precautionary Approach among the fora that we reviewed, chose to define limit reference points in terms of the maximum fishing mortality and minimum biomass thresholds associated with stock collapses rather than with maximum sustainable yield (MSY). Such limit reference points were considered entirely within the scientific purview and did not need to be discussed with management agencies. Consequently, ICES took it upon itself to set limit reference points.

To have a high probability of avoiding the limit reference points and the associated stock collapses, management action must be taken before the limit reference points are approached. However, deciding on precautionary reference points where management action was required in order to

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avoid the limits is not only a scientific question related to the uncertainties in the assessment and management implementation, but is also a sociopolitical question related to the degree of risk acceptable to the fishery management agency. Therefore, ICES *suggested* precautionary reference points. These are still to be agreed to by the fishery management agencies, but since 1998, ICES has been using both the limit and the precautionary reference points to frame its advice to the European Commission, the International Baltic Sea Fisheries Commission, the Northeast Atlantic Fisheries Commission, and the North Atlantic Salmon Conservation Organization. Most suggested that these precautionary reference points still need to be formally accepted.

The Northwest Atlantic Fisheries Organization developed a system of reference points closely related to the ICES one with the exception that it adheres strictly to article 7 of Annex II of the UN Agreement and sets the fishing mortality corresponding to the MSY (F_{MSY}) as a limit reference point. The International Commission of the Conservation of Atlantic Tunas has not yet made a decision on targets and limit reference points, but its convention specifies MSY as a management objective.

In these fora, as well as in Canada and the United States, the adoption of reference points (or of overfishing definitions in the United States) is closely linked to preagreement on decisions to be made when the reference points are reached. In other words, agreeing on the reference points implicitly brings with it agreement on harvest control rules. The details vary between the various fora, but the basic framework is similar: taking uncertainty into account, assess the size of the stock and associated fishing mortality, compare with reference points in terms of F (where F is the instantaneous rate of fishing mortality) and biomass, and make decisions on management measures. An interesting modification is being developed in Canada where several indicators other than F and biomass are evaluated for their usefulness in making management decisions (Halliday 2000).

The International Pacific Halibut Commission (IPHC) is one of the rare fishery management organizations whose activities have met with success. The resource has gone through natural cycles, but the productive capacity has been protected and the IPHC has been able to reduce or raise catch as the biological health of the population fluctuated. While IPHC has not *formally* adopted the Precautionary Approach, the management strategy followed by IPHC is chosen (and periodically reevaluated) in a way that is consistent with the Precautionary Approach, that is, by analysing likely consequences of alternative control rules under different scenarios about future trends in productivity consistent with historical experience (Sullivan et al. 1999; Parma 2000). Control rules involving target harvest rates and minimum size limits have been adopted after open discussions among scientists, managers, and stakeholders, which attempt to account for the different sources of uncertainty affecting management decisions. While no definition of overfishing has ever been attempted, and limit reference points are not part of the implemented harvest control rule, target harvest rates below F_{MSY} have been chosen so as to lower the risk of reducing biomass below historical records, even though recruitment overfishing was never experienced at those low biomasses. Conservative targets have been supported by the fishing industry, as fishers are the first interested in avoiding the low biomasses (and catch rates) experienced in the past.

Generally, progress has been led by science with significant developments in quantifying uncertainty, defining reference points, and proposing harvest control rules. Fishery management agencies have not been particularly proactive. Yet, it is precisely because of large uncertainties in fishery science and management implementation that fishery management itself should be more precautionary.

Towards a broader implementation of the Precautionary Approach

The initiatives described above to implement the Precautionary Approach have been mostly driven by fishery science with its traditional emphasis on fish population dynamics and reference points. It is therefore not surprising that the focus has been on protecting the fish resources and the environment that they live in. As a consequence, most advances have been made in the technical aspect of developing harvest control rules based on conservative reference points for fishing mortality and stock biomass and on how to use them to provide fishery management advice in the context of the Precautionary Approach. From a practical perspective, such emphasis in the implementation of the Precautionary Approach has lead to more stringent advice, sometimes with implied severe consequences for the fishing communities. Indeed, the implementation of the Precautionary Approach by ICES in its advice was harshly criticized by the U.K. House of Commons Select Committee on Agriculture for not taking into account the effects on the fishing industry (http://www.publications.parliament.uk/pa/cm199899/cmselect/cmagric/141/14105.htm#a5).

The Precautionary Approach to fisheries management requires much more than the implementation of precautionary harvest control rules. Its scope should be much larger (Richards and Maguire 1998), emphasizing that a precautionary system needs data collection, evaluation of the results of past management, response mechanisms to adjust management action as appropriate, effective enforcement of regulations, and a process that facilitates communication and fosters cooperation among the different sectors involved with and affected by management. Such a precautionary system would be more consistent with the early description of the Precautionary Approach provided by FAO (1996) than most implementations so far.

The international instruments do not explicitly state the scope of the Precautionary Approach, but they generally refer to it in the context of protecting the resources and the environment. The broader context, however, is sustainable development with its cornerstone concept of intergenerational equity. An interesting discussion of intergenerational equity can be found at http://www.unu.edu/unupress/unupbooks/uu25ee/uu25ee0z.htm (p. 5) where the three principles of conservation of options, conservation of quality, and conservation of access are proposed key elements of the concept. "The proposed principles recognize the right of each generation to use Earth's resources for its own benefit,

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but constrain the actions of the present generation in doing so. Within these constraints they do not dictate how each generation should manage its resources. They do not require that the present generation predict the preference of future generations, which would be difficult if not impossible." This implies sustainable use, consistent with our view that the goal of fisheries management is not to conserve fish stocks for conservation sake but rather to achieve long-term sustainability of both the fish resource and the fishing communities. Therefore, we believe that the protection of fishing communities is a component of the Precautionary Approach that should be made more explicit. This is consistent with the proposed conservation of options principles where "Conserving the diversity of natural and cultural resource bases is designed to give our descendants a robust and flexible heritage with which to try to achieve a decent and healthy life." (http://www.unu.edu/unupress/unupbooks/uu25ee/uu25ee0z.htm, page 5). Standard 8 of the U.S. Magnuson-Stevens Fishery Conservation and Management Act requiring that, consistent with the conservation requirements of the law, the plans provide for the sustained participation of fishing communities and minimize adverse economic impacts on these communities is consistent with this principle.

Protecting the harvestable resources could be argued to be sufficient to protect the fishing communities de facto. After all, it is necessary to have resources to exploit in order to have fishing communities. But this is a specious argument. The exclusive focus on the resource would naturally lead to choosing management measures that have the highest probability of protecting the resource, even though some other measure, with perhaps marginally smaller probability of resource protection, would have considerably less negative impacts on the communities. Explicit consideration of the fishing communities is consistent with the proposal for fishery management science by Stephenson and Lane (1995) to replace the excessively biological orientation of traditional fishery science and with the proposal by DeYoung et al. (1999, p. 114) that the "management objectives must include not only the central and overriding objective of maintaining ecosystem integrity, but also the secondary objectives of social and economic well-being."

The exclusive focus on the resource makes us forget the real objective of fishery management: to achieve long-term sustainable fisheries that provide jobs, economic opportunity, food, and stable communities. Some countries and jurisdictions may emphasize jobs, others may emphasize economic profit, and others food production, but by and large the purpose of fisheries is to catch fish on a sustained and profitable basis. If this perceived main objective is met, then we have greater confidence that intergenerational equity will also be achieved.

Risk

Risk assessment

Risk assessment involves evaluation of the consequences of alternative management actions under uncertainty and has been applied almost exclusively to decisions regarding total allowable catches. The following example illustrates the dilemma between risk to the fishery and risk to the fish stock. Imagine a fishery where the stock is approaching a historically low biomass following several years of low recruitment and high exploitation rates. Scientific analysis suggests that if fishing is not curtailed, there is a 50% probability that the stock will collapse, and the fishery would therefore cease for lack of fish, perhaps for an extended period. In this hypothetical example, the 50% probability of stock collapse unless fishing mortality is reduced to close to zero is the average of the risks estimated under two hypotheses given equal credibility. Hypothesis A: recruitment is closely related to spawning stock biomass; because spawner abundance has been reduced by fishing, recruits have become progressively less numerous in a vicious circle that will end with severe stock depletion and complete closure of the fishery. Hypothesis B: recruitment is environmentally driven; the experienced poor recruitment is the result of prolonged unfavourable environmental conditions; strong year-classes will only be produced when environmental conditions improve.

As implied by the fishery management objectives stated earlier, fishery management wants to avoid the destruction of the fishery, the loss of jobs, the bankruptcies, and personal distress associated with a major fishery closure. If the fishery is closed in a "precautionary" fashion, there is a 100% probability that the fishery is destroyed in the short term. If continued fishing is allowed, there is a 50% probability under the scenarios above that the fishery will be destroyed in the short term. For most "traditional" fishery management arrangements, the answer would seem clear: take the chance that hypothesis B is correct rather than destroying the fishery for sure by halting fishing. While this may appear to be an adequate response to short-term socioeconomic pressures, it may only result in a more acute crisis later on (National Research Council (NRC) 1998*a*).

In reality, the situation would never be that simple. Longer-term consequences, both biological and to the fishing communities involved, would need to be taken into account. If recruitment did depend on spawning biomass (hypothesis A), the fishery could reopen in the medium to long term, yielding higher catches than heretofore. Under the close fishery option, the fishery would soon reopen for stocks with high growth rates and revenues would increase rapidly. For stocks with low growth rates, however, the recovery time could be so long that the fishing communities would not be able to survive to benefit from the recovery. Under the environmentally driven hypothesis, on the other hand, there still could be longer-term benefits in reducing fishing in order to take better advantage of good recruitment when environmental conditions improve. Another complicating factor is that even if recruitment were indeed mostly controlled by the environment, it would seldom be the case that a biological collapse could be totally ruled out if fishing continued as in the example above. There has to be some low spawning biomass below which recruitment would be seriously compromised no matter what the environmental conditions are. Very little is known about how populations behave at very low abundance, and quantifying the biological risks as the "probability of collapse" is an oversimplification. The severity of the collapse and the probability of recovery from it would also be affected by the management decisions in ways that would be difficult to anticipate. Experience with some of the major fishery collapses shows that it often takes at least a decade

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for stocks to recover (Georges Bank herring, North Sea herring, Northern cod).

Risk management

At best, risk assessment will tell us the appropriate probabilities and details about the consequences of various management actions, including no action. But in the end, the choice will be a gamble — how will the fishery management agency balance the risk of *assured* social and economic dislocation if the fishery is closed against the *possible* longer-term social economic dislocation of a fishery-induced stock collapse and the biological threat of such a collapse. Risk analysis and risk assessment do not provide better policy choices, they only evaluate them. It is therefore necessary to move from risk assessment to risk management.

Fishing can be regulated by technical measures (gear type, mesh sizes, time and area closures, etc.), by input controls (number, type and size of vessels, number of gear or time units each is allowed to fish, etc.), and by output controls (the various forms of catch controls including individual, vessels, and community quotas whether transferable or not). One or more elements of each approach are normally used and it is not uncommon to have a quota-regulated fishery also including time and area closures, gear type, and mesh size regulations as well as an upper limit on days at sea. All these approaches are compatible with risk management, but their usage in the past has sometimes increased the risk to fishing enterprises rather than decreasing it.

Fishery management is not the only form of human activity that has to make decisions in the face of uncertainty. Farming, the stock market, and the medical field, to give a few examples, have to make decisions in the face of very high uncertainty and possible severe adverse consequences. These fields have already moved beyond risk assessment to include risk management. The simplest form of risk management is risk sharing with common mechanisms including diversification of portfolios in the stock market. Insurance is a second form of risk management in which the risk of loss is shared with the broad pool of insurance purchasers.

Management of risk has been given relatively little consideration in the fisheries literature. Emphasis has been on the need for economic diversification and provision of nonfishery employment alternatives to relieve pressure on the fish resources as primary sources of livelihood (Smith 1981; Charles 1994). Portfolio theory has recently been applied also to support diversification of tools used in fisheries management, such as the use of marine reserves as an insurance against failure of conventional methods based on effort or catch controls (Lauck 1996; Lauck et al. 1998). Our focus here is rather on the need to diversify fishing opportunities available to the industry. This relates to enhancing the mobility of fishing capital and labour, which in turn should ameliorate "the exit problem" (John 1994) when fishers are locked into a fishery for lack of alternative species to exploit (possibly because of limited-entry programs). Risk management can take several forms, such as insurance to individual fishers, directly or through private companies, as is already done for crop insurance for farmers. Such insurance schemes would take into account the expected variability in abundance, price, and whatever other variables fishers wished to be insured against. Interestingly, risk management appears to have been better studied with respect to aquaculture (Bacon et al. 1993; Paquotte and Antona 1993; Secretan and Nash 1989) than to capture fisheries.

Diversification, herein referred to as portfolio management, appears to be a particularly effective means of managing risk in fisheries. Artisanal fishers often fish a wide range of species and stocks, so that when abundance or price is bad for one species the effort can be shifted to another one. This is becoming increasingly difficult, however, because governments' limited-entry programs and capacity adjustments through fishing licenses withdrawal force fishers to become specialized in one or in a small number of fisheries, thereby preventing them from using a traditional means of risk management through diversification. This, however, is not so much a problem with limiting entry per se, which is essential if harvesting is to be controlled, but in the way entry has been limited. For many fisheries, limited-entry systems have simply restricted participation to historical fishers once overcapacity had already been reached and limited vessels to operate only in a fishery for which they have a license. It is usually economically impossible to afford licenses for multiple fisheries. A more sophisticated and workable limited-entry system that would maintain greater flexibility includes entry and exit rules so that it is possible to control the number of participants without eliminating the possibility of moving from one fishery to another. Individual transferable quota systems have entry and exit rules set by the marketplace and need not provide any barriers to movement of vessels between fisheries. Individuals have the option under most systems of using their fishing skills in one fishery while owning quota in other fisheries and leasing it out. Most fishers do not do this, but they do have the option to do so. Fishery cooperatives, such as those recently set up in Alaska under the American Fisheries Act, control entry and exit decisions for individual participants through the cooperative structure.

Portfolio management seems a logical choice given that the overall productivity of fishery systems is more stable than individual species are. Consider, for example, that the economic value of fishery products landed in eastern Canada, split into three major groups, groundfish, pelagics, and shellfish (http://www.ncr.dfo.ca/communic/statistics/stat_e.htm), has been stable or increased since 1989. The nearly complete closure of the groundfish fishery, which has led to a billion dollar (Canadian) per year compensation package to the fishers and fish plant workers, did not cause a decrease in the total value of fisheries landings in eastern Canada since 1992, on the contrary. The boom in catch and economic value of snow crab, shrimp, and lobster has more than made up for the loss of groundfish. In New England, the value of fisheries has remained relatively high, although not as high as it would be if the overfished stocks were fully rebuilt (Edwards and Murawski 1993), partly by switching to a much larger range of target species and diversification into other fisheries and partly because of large increases in prices over the last two decades. Other examples are numerous. While the crab fisheries of Alaska collapsed, the salmon and groundfish fisheries blossomed. While chinook and coho salmon in British Columbia collapsed, sockeye, pink, and chum salmon did well.

Thus, even though as a whole, the "fisheries" of eastern

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Canada and New England have been stable, the communities have seen enormous social and economic changes. In Canada, while the fishers catching snow crab and shrimp have enjoyed great success, their neighbours who used to fish groundfish have had to diversify into nontraditional groundfish species such as rays and monkfish and downsize their operations considerably or leave the industry altogether. Arguably, the problems faced by Canadian east coast groundfish fishers would have been less severe if they had had the possibility of diversifying in the lucrative shrimp and snow crab fisheries, which they were prevented from doing in the early years of the closure. Lately, the Canadian Department of Fisheries and Oceans has attempted a better sharing of the wealth through issuance of new licenses for shrimp or snow crab fishing or through other mechanisms for revenue sharing. Application of the Precautionary Approach through appropriate controls in place early in the development of the groundfish fishery, and with industry and political support, could have probably avoided large declines and collapses. With adequate risk management, their effects would have been minimized when they did occur. Individual fishers already practice risk management in one way or another to the extent that it is possible in the fishery management processes that they are involved in. They have to hedge against natural changes in resource abundance and decreases in price, but also against government-driven risks. The purse seine fisheries for herring roe on the west coast of North America present a very high risk. The fisheries are very short, sometimes lasting no more than 15 min, and it is common for the competing fishing vessels to either do very well and capture a large number of fish — individual vessels have caught $1 million worth of fish in a single set of the net — or more commonly catch nothing. Not too surprisingly, many west coast herring fishers choose to manage the risk by joining various forms of catch collectives: individuals with a high risk aversion might pool their catch among many vessels, while risk-prone individuals might do no pooling.

Another mechanism for risk management is community-based management in which a community has user privileges, either by tradition or by legal right, on some fish resources or fishing grounds, and thus the entire community shares risk. Some traditional fisheries management systems engage in this (Berkes 1989; Johannes 1998). The advent of community development quotas (CDQs) in Alaska (NRC 1999), now being considered elsewhere in the United States, provides a possible mechanism. With CDQs, communities are given the right to harvest a fixed amount of fish and the community can either allocate the catch among its residents or lease the fishing rights. CDQs are currently in place for Pacific halibut, sablefish, and pollock in Alaskan communities. If communities owned a mixed portfolio of fishing rights, then the community, as a whole, would be buffered against fluctuations in harvest or price in any individual species or group of species.

The original New Zealand individual transferable quota (ITQ) system in which individual fishers owned the right to harvest a fixed amount of a given species was an attempt at risk management by the government. If the fishery management agency determined that the total allowable commercial catch needed to be lowered, the government would buy back quota at market rates. If there was the potential to increase total commercial catch, the government auctioned off the additional quota. This system buffered the commercial fishers from fluctuations in abundance in that only those people willing to sell their quota would have to catch less fish in the future, but it did not provide protection from fluctuations in price or costs of fishing. Because the original experiment was terminated prematurely, the behaviour of the market in the case of a major fishery decline requiring a nearly total halt to fishing remains unknown.

In principle, in the original New Zealand ITQ fishery, the government managed the risk and protected the fishers from fluctuations in allowable harvest. In practice, the New Zealand government did auction additional quota when it raised allowable catches on hoki and orange roughy, but when quota reductions were deemed necessary, the government was unwilling to purchase quota back and instead changed the laws so that the fishers owned a percent share of the total allowable commercial catch rather than an absolute amount. This was effectively transferring the risk from the government to the fishers. This change in the law was the subject of litigation, and fishers were eventually compensated for a period of time for any quota reductions.

Thus, the original New Zealand ITQ experiment may be viewed as a failed attempt at governmental risk management. No analysis of the revenues from the New Zealand government ITQ system is publicly available, but could it be possible that the income from quota sales balanced the expected costs from quota reductions and the government simply took the opportunity to take a quick profit, like many investors would?

However, the New Zealand ITQ system, like the ITQ systems in many other places, does provide several avenues for individual-based risk management. First, an ITQ holder is assured of his or her share of the total allowable catch and thus is shielded from many risks in an "Olympic" system where each fisher has to "race" to catch his share before the total allowable catch is exhausted. Equipment breakdown and illness pose particular risks in "Olympic" systems because they prevent individual fishers from partaking in the "race", while the ITQ owner has the right to harvest the fish no matter how long it takes. ITQ systems also provide an opportunity for risk management by permitting individuals to split their ownership across different species. Thus, a fisher who owns quota in one species can in principle reduce risk by buying or leasing quotas in other species and perhaps reducing ownership in his own species. Many New Zealand firms now hold very diverse portfolios of quota, buffering them from fluctuations in total allowable commercial catch of individual species. We do not know if this is a common practice among individual fishers and quota holders in New Zealand.

The overshooting of trip limits or allocation normally results in the offender being fined, sometimes substantially. ITQ systems also protect against the risk of being fined for having overfished one's quota by allowing one to buy quota on the market.

Some form of risk management therefore appears to be compatible with most management systems currently in place. We believe that individual fishers, and therefore the communities that they live in, would be better protected if

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current fishery management arrangements concentrated their effort explicitly on devising ways to implement efficient risk management.

Implementation of risk management

The current situation in fishery management agencies is the result of decades of evolution. The extension of fishery jurisdiction in 1976–1978 saw a rapid expansion of the fishery management mandate of responsible agencies in both Canada (Department of the Environment 1976) and the United Stated. A standalone department was created in Canada in 1977 with considerable new resources to tackle the daunting but potentially very rewarding challenge of managing Canada's fisheries (Parsons 1993). Before extension of jurisdiction, active management was essentially limited to a few offshore fisheries under the purview of the International Commission for Northwest Atlantic Fisheries, but after extension of jurisdiction, scientists and resource allocation officers were identified for *all* resources, including small inshore stocks.

The main impediment to implementing the Precautionary Approach and risk management is the inertia in the fishery management process itself and the fact that most fisheries are either overcapitalized or overharvested. Excess capacity to harvest the available resource undermines diversification of fishing effort to manage risk, particularly because of the absence of entry and exit mechanisms mentioned above. For overfished stocks where severe declines are likely to occur or already have, the risk could be already out of control and it might be difficult to effectively manage it. On the other hand, crisis situations sometimes make it easier to implement drastic solutions.

A related point, illustrated perhaps by the original New Zealand ITQ program described above, is that governments are probably not the best party to implement risk management. They should, however, design and implement management systems that allow it to happen and encourage its implementation. Individual businesses, communities, or sectors should manage risk with systems tailored to their own needs.

Limited-entry systems have usually been introduced into fisheries on a catch history basis, often a recent catch history. Thus, only individuals who have been actively involved in a particular fishery in the recent past have been given limited-entry licenses. Managers have often forced mixed-gear boats to choose a single gear; for example, in the Btitish Columbia salmon fishery, mixed troll/gillnet boats have been systematically eliminated from the fishery by licensing. In other cases, such as on the Atlantic coast, unused licenses were retired in the early 1990s when the groundfish collapse was well under way in order to reduce latent fishing capacity. In a sense, this measure was penalizing those that had *not* contributed to groundfish (over)exploitation.

Economic pressures, linked to the fishery management measures in place, also forced specialization: as fishing efficiency increased and fishing seasons have become shorter, individuals needed to increase their specialized capital in order to maintain their share of the catch. Mixed-gear boats simply could not effectively compete with the newer specialized boats.

Government institutions also promote specialization: research and management are often divided along the lines of types of fisheries, i.e., groundfish, pelagics, invertebrates. This promotes the mindset of specialization (i.e., managers thinking of "their" fishers), and in fisheries where understanding the government system is important to success, individuals have increasing difficulty in balancing a portfolio across different types of fishing. By the early 1980s, the Department of Fisheries and Oceans could count on a large workforce of fishery managers (resource allocation officers), fishery officers (monitoring, control, and surveillance), and fishery scientists, dominated by biologists but including economists as well. The responsibilities were largely structured by species, which meant that in each administrative region (there were four on the Canadian Atlantic coast), there was one or more lobster scientists, scallop scientists, shrimp scientists, cod scientists, herring scientists, etc., and resource allocation officers by species groups (groundfish, pelagics, invertebrates). This meant that the small-scale inshore fisher who had implemented portfolio management and had fishing licenses for groundfish, herring, mackerel, lobster, and perhaps scallop or snow crab had to deal with at least two resource allocation officers and probably more than four scientists. By the mid-1990s, after the groundfish stocks collapsed, strict application of limited-entry licensing led to the situation described above where in many villages, groundfish fishers had incomes from government that put them barely above the poverty line, while lucky fishers who held on to their now very lucrative fishing licenses for invertebrates earned up to a million dollars a year before the recent decrease in the price of snow crab.

The trend towards area licensing reduces the options for risk management, as it can result in fishers being locked into a location when conditions there deteriorate (John 1994). It is the geographical equivalent of limited entry on a species basis. In Alaskan and now Canadian fisheries for Pacific salmon, individual licenses are limited to specific areas. In former times, individuals could manage their risk by moving from area to area; now they generally must choose a single or small number of areas to fish, which in turn forces higher risk upon them. Area licensing has recently been introduced into the British Columbia groundfish fishery.

Other trends in fisheries management force specialization and thus increase the risk rather than improve on the ability to mitigate against risk. Obviously, catch fluctuations for individuals would be lowest if all fishers had a stake in a wide range of fisheries. However, many aspects of fisheries management are facilitated by smaller groups of stakeholders and therefore act counter to this. It is our experience that when dealing with smaller number of stakeholders, there is more long-term perspective, individuals recognize the self-interest in obeying regulations, and it is easier to discuss and implement new and different management approaches. The smaller and more uniform the stakeholders, the fewer internal conflicts there are between individuals, and the more likely the stakeholders are to cooperate. Unfortunately, the smaller the stakeholder group, the higher the risk each individual stakeholder must take because they must be more specialized in species and area.

Risk can be decreased by using conservative harvest guidelines, but it can and should also be managed. One way

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of reducing risk is by reducing fishing pressure in order to have larger average stock sizes, which would serve as a buffer for natural fluctuations. This may not prevent naturally induced "collapse" but it would better utilize the resource base and would provide a more stable planning environment for the fishing and marketing interests. In times of hardship, whether a result of overfishing or naturally induced, maintaining a diversified portfolio of options open to the fishing industry should alleviate social and economic tensions and facilitate implementation of needed fishing restrictions.

Discussion

Most progress in the implementation of the Precautionary Approach has been in the adoption of conservative harvest guidelines that would prevent overfishing and stock collapses. However, society's interest is also with the fishers, the fish plant workers, and the communities who depend on them. We submit that fishery management on the Canadian east coast should be considered to have failed not only because fish stocks have collapsed, but also because it failed to provide sustained and dignified employment to fishers and fish plant workers and because it created social inequities and social unrest in fishing communities. Indeed, the biological productivity of the east coast resources could have provided for sustainable fishing communities if the management system had been properly structured. We propose that portfolio management, where individual fishers are allowed to fish several species rather than being restricted to only one or a few species group such as groundfish, would have diverted fishing effort to other species and might perhaps have prevented total closures. Even if portfolio management had not had such desirable biological side effect, it would have certainly led to more equitable income distribution and less social unrest.

If the implementation of the Precautionary Approach continues to be a techno/scientific/bureaucratic-driven process, and the well being of fishing communities is not taken into account explicitly, the process will fail. Therefore, implementing the Precautionary Approach must imply the application of risk management to reduce the risk of collapse of fishing communities.

What should fisheries managers do? Should the trend towards small stakeholder groups, area licensing, etc., be reversed and should we go back to encouraging generalization rather than specialization? We doubt that there is any widely applicable solution. We have discussed a mixed bag of tools that can be used for risk management, but certainly the time is right for the development of novel approaches, given the serious downsides of the prevailing trend towards specialization. We suggest that management agencies put the topic on their political agenda — we have seen little evidence of consideration of risk management in major fisheries, with manager and politician interests focused primarily on avoiding risk rather than managing it.

Risk may be assessed and decreased, but not avoided. The lessons of the major fish collapses of the last 30 years (Walters and Maguire 1996) and the growing recognition of limitations of conventional assessment methods and management tools (NRC 1998*b*) and of the great uncertainty surrounding management decisions suggest that risk is unavoidable — at best, we can understand the odds of the gambles that we are taking, but fisheries management is a gamble and on occasion, we are going to have stocks in trouble. If we are to succeed at management — if we are to maintain stable fishing communities — we have to begin to manage risk.

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Conservation biology of marine fishes: perceptions and caveats regarding assignment of extinction risk

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Abstract: Quantitative criteria used to assign species to categories of extinction risk may seriously overestimate these risks for marine fishes. Contemporary perception is that marine fishes may be less vulnerable to extinction than other taxa, because of great natural variability in abundance, high fecundity, rapid population growth, and an intrinsically high capability of recovering from low population size. Contrary to perception, however, there appears to be generally little theoretical or empirical support for the hypotheses that marine fish are more likely to experience large reductions in population size, to produce unusually high levels of recruitment, to have higher reproductive rates, or to recover more rapidly from prolonged population declines than nonmarine fishes. Although existing population-decline criteria may not accurately reflect probabilities of biological extinction, they do appear to reflect the converse—population recovery. Insufficient support for contemporary perceptions of their susceptibility to extinction, coupled with caveats associated with the assignment of extinction risk, suggest that significant increases in the population-decline thresholds used to assign marine fishes to at-risk categories would be inconsistent with a precautionary approach to fisheries management and the conservation of marine biodiversity.

Résumé : Il est possible que les critères quantitatifs qui servent à placer les espèces de poissons marins dans les diverses catégories de risque d'extinction surestiment grandement ces risques. On croit couramment que les poissons marins courent moins de risques d'extinction que les autres taxons, à cause de la grande variation dans leurs densités, de leur forte fécondité, de leur croissance démographique rapide et de leur habileté intrinsèque marquée à récupérer après un déclin de densité. Cependant, contrairement à ce que l'on pense, il a peu de fondements théoriques ou empiriques aux hypothèses selon lesquelles les poissons marins sont plus sujets à de fortes réductions de densité que les poissons non-marins, que leur recrutement peut atteindre des valeurs exceptionnellement élevées, que leurs taux de reproduction sont plus élevés et que leur récupération après un déclin est plus rapide. Bien que les critères actuels de déclin des populations ne reflètent pas correctement la probabilité d'extinction biologique, ils semblent mettre en lumière l'inverse, soit la récupération des populations. Puisque les perceptions courantes de la susceptibilité des poissons marins à l'extinction ne sont pas assez solidement démontrées et compte tenu des mises en garde inhérentes à l'établissement du risque d'extinction, un relèvement substantiel des seuils de déclin de population établis pour les diverses catégories de risque serait incompatible avec une attitude prudente dans l'aménagement des pêches et la conservation de la biodiversité marine.

[Traduit par la Rédaction]

Introduction

Worldwide overexploitation of commercially harvested fishes raises the question of whether the often spectacular declines in abundance associated with fishery collapses have significantly increased the extinction probability of targeted (e.g., Atlantic cod, *Gadus morhua*; IUCN 1996) and incidentally harvested (e.g., barndoor skate, *Raja laevis*; Casey and Myers 1998) marine species (Reynolds and Mace 1999; Roberts and Hawkins 1999; Musick et al. 2000). This is reflected in part by the work of national and international agencies responsible for assigning risk or threat categories to potentially endangered taxa. In 1996, the International Union for the Conservation of Nature (IUCN) assigned Atlantic cod to their "vulnerable" threat category (IUCN 1996). The same status was applied 2 years later in Canada by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) (Shank 1999). By the end of the 20th century, marine fishes designated as vulnerable by IUCN included haddock, *Melanogrammus aeglefinus*; Atlantic halibut, *Hippoglossus hippoglossus*; and yellowtail flounder, *Pleuronectes ferrugineus*. In addition to Atlantic cod, COSEWIC identifies Bering wolffish, *Anarhichas orientalis*, and Pacific sardine, *Sardinops sagax*, as marine fishes of "special concern" (as of May 2000, this term replaces the vulnerable category; COSEWIC 2000) (Shank 1999).

However, some criteria applied by national and international agencies responsible for assigning risk categories (Table 1) may significantly overestimate extinction threats to marine fishes and should, perhaps, be modified significantly to account for perceived differences between marine fishes and the other taxa to which these criteria are regularly applied, for example, plants, mosses, lichens, terrestrial ani-

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Table 1. Summary of the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) and the International Union for the Conservation of Nature (IUCN) risk categories and criteria. For interpretation guidelines, refer to IUCN (1999).

Criteria A through F	Critically endangered (IUCN)	Endangered (IUCN/COSEWIC)	Threatened (COSEWIC)/ Vulnerable (IUCN)
A. Declining population:			
a population decline rate, in 10 years or 3 generations, of at least	80%	50%	20%
B. Small distribution and decline or fluctuation:			
either extent of occurrence (km^2) of	<100	<5000	<20 000
or area of occupancy (km^2) of	<10	<500	<2000
and two of the following three:			
1. *either* severely fragmented into isolated populations with a low probability of recolonisation, if once extinct; *or* known to exist at locations numbering	1	≤5	≤10
2. continuing decline at any rate *in any of the following*:			
a. extent of occurrence			
b. area of occupancy			
c. area, extent, and (or) habitat quality			
d. number of locations or populations			
e. number of mature individuals			
3. a greater than 10-fold fluctuation *in any of the following*:			
a. extent of occurrence			
b. area of occupancy			
c. number of locations or populations			
d. number of mature individuals			
C. Small population size and decline:			
number of mature individuals	<250	<2500	<10 000
and one of the following two:			
1. decline rate of at least	25% in 3 years or 1 generation	20% in 5 years or 2 generations	10% in 10 years or 3 generations
2. continuing decline at any rate and			
either (*a*) fragmented with numbers of mature individuals in all populations of	≤50	≤250	≤1000
or (*b*) all mature individuals existing in a single population			
D. Population very small or restricted:			
either (1) the number of mature individuals is	<50	<250	<1000
or (2) the population is susceptible†	na	na	
E. Quantitative analysis:			
indicating the probability of extinction in the wild to be at least	50% in 10 years or 3 generations	20% in 20 years or 5 generations	10% in 100 years
F. Rescue-effect adjustment‡:			
if there is significant and on-going immigration from cross-border populations, downlist one category			

*Species and populations of Special Concern are those deemed particularly sensitive to human activities or natural events but are not Endangered or Threatened (COSEWIC 2000).
†For the threatened (COSEWIC) and vulnerable (IUCN) categories, the criterion is area of occupancy <100 km^2 or number of locations <5.
‡Used only by COSEWIC.

mals, and nonmarine fishes. It has been suggested that, because of their perceived great natural variability in abundance, high fecundity, rapid population growth, and remarkable ability to recover from population collapse, marine fishes may be less vulnerable to extinction than other taxa (e.g., Hudson and Mace 1996; Matsuda et al. 1997; Musick 1999; but see Carlton et al. 1999). Indeed, there appears to be nothing intrinsic to exploited marine fishes to prevent them from increasing at low population sizes (Myers et al. 1995*a*), although the generality of the conclusion that per-capita reproductive success increases at low population levels may not be as widespread as previously thought (Leirmann and Hilborn 1997; Shelton and Healey 1999; Frank and Brickman 2000).

My purpose here is to explore the theoretical and empirical bases underlying contemporary perceptions of the resilience of marine fishes to population collapse, relative to nonmarine taxa. The paper was motivated by several factors, including: (*a*) proposed national endangered-species legislation in Canada, (*b*) increased concern that extinction threats to marine species merit attention (Carlton et al. 1999; Roberts and Hawkins 1999; Musick et al. 2000), (*c*) unresolved

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arguments that marine fishes warrant at-risk criteria that differ from nonmarine fishes (Musick 1999; Powles et al. 2000; see Reynolds and Mace 1999), and (*d*) the failure of many marine-fish populations to recover from collapse, for example, Northwest Atlantic cod (Hutchings 1999; Shelton and Healey 1999) and Iceland spring-spawning herring, *Clupea harengus* (Myers et al. 1995*a*).

Perception: marine fishes experience greater natural fluctuations in abundance than nonmarine fishes

If a reliable metric of abundance indicates that a population or stock (species in the case of IUCN) has exceeded a specific percentage decline over the longer of 10 years or three generations, the taxon can be assigned to one of several risk or threat categories (e.g., vulnerable – special concern, threatened, endangered, critically endangered). To date, this is the criterion by which IUCN and COSEWIC have assigned at-risk categories to marine fishes (see criterion A in Table 1). The population-decline criterion may, however, seriously overestimate extinction risks for marine fishes, because (*a*) large reductions in population size can represent a primary goal of fisheries management and (*b*) marine fishes are perceived to be naturally more variable and more likely to experience large reductions in abundance than other taxa.

The first component of this assertion is based on the prediction that a substantive reduction in the size of an unfished population must be effected before the maximum sustainable yield (MSY) for that stock can be harvested. The argument can be made, then, that a rapid decline in a commercially exploited marine-fish stock might simply represent the end point of a management goal, and need not be indicative of a population under threat of extinction (Hudson and Mace 1996; Musick 1999; see Reynolds and Mace 1999). Such an argument might have merit, if temporal trends in abundance estimates of marine fishes generally included virgin-stock sizes. However, given the low probability of knowing the virgin-stock size for most marine fish species, the MSY-based argument, in the context of overestimating extinction risks for marine fishes based on criterion A (Table 1), would seem to be moot for all but new fisheries.

New fisheries, for which virgin biomass might conceivably be estimated, may indeed be subject to a management-directed reduction in biomass to increase productivity, although one would be hard-pressed to identify many current examples. Under these circumstances, according to existing criteria, if a population decline was sufficiently large and sufficiently rapid, the stock may be subject to an at-risk designation. This need not, however, be interpreted as inappropriate from a management perspective, particularly if the time frame during which the at-risk designation would be invoked was interpreted as a "probationary" period. If managers were successful in preventing further decline, the stock would eventually be delisted. The history of fisheries overexploitation (Smith 1994) suggests that such a probationary period would not be undesirable.

The second component of this perception appears, at first glance, compelling. There is a general impression that population sizes of marine fishes are more variable than those of freshwater and anadromous fishes (e.g., Musick 1999; Powles et al. 2000), leading to the possibility that 10-year or three-generation declines of more than 50 or 80% (see criterion A in Table 1) might simply represent "natural" fluctuations in abundance rather than increased risks of extinction. Importantly, however, it is not at all clear how one can reliably distinguish natural from fishing-induced fluctuations in abundance for commercially exploited species.

The observation that recruitment is highly variable in marine fishes was raised by the IUCN in its evaluation of the degree to which its criteria should be applied to marine fishes (Hudson and Mace 1996), although there is no evidence that recruitment variability in marine fishes exceeds that of anadromous fishes (Mertz and Myers 1996). In any event, it is the *reproductive* component of the population to which the IUCN and COSEWIC criteria apply. With reference to criterion A (Table 1), one can ask, then, whether marine fishes are more likely to experience large reductions in spawner population size than nonmarine fishes.

To address this question, I consulted the summary of worldwide spawner and recruitment data originally compiled by Myers et al. (1995*b*) and maintained by R.A. Myers (Department of Biology, Dalhousie University, Halifax, NS B3H 4J1, Canada) at http://fish.dal.ca/welcome.html. I used these data to quantify, and to compare among three groups of fishes (iteroparous marine fishes, iteroparous freshwater fishes, and semelparous salmonids), the frequency with which stocks experienced maximum three-generation declines (approximated as both 15 and 20 years for marine and iteroparous fishes) in spawner abundance or biomass of <50% (small decline), 50–79% (medium decline), and 80% or more (large decline).

Data were available for a minimum of 15 consecutive years or three generations for 163 stocks among 65 species of marine fishes, 106 stocks among five semelparous salmonids (*Oncorhynchus* spp.), and 14 stocks among seven iteroparous freshwater species. There were no significant differences in the incidence of small, medium, and large declines between marine and nonmarine fishes (Table 2; G tests, $p > 0.05$ for all possible comparisons), although the power of some comparisons was reduced by the relatively small sample of freshwater-fish populations. Nonetheless, comparing marine fishes with semelparous salmonids, for which sample sizes were large, the incidence of large (≥80%) reductions in population size was actually higher for salmonids, being 30 and 38%, respectively. Thus, based on data available for 283 stocks, there is no empirical support for the perception that the spawning component of marine fishes normally experiences declines with greater frequency than that of nonmarine fishes.

Perception: marine fishes are more productive and are more likely to produce unusually high numbers of offspring than other taxa

The perception that marine fishes are more productive and more resilient than other taxa can be traced to what might be termed the "ghost of inexhaustibility past" (sensu Connell 1980), which evidently continues to haunt some into concluding that the production of hundreds of thousands, often millions, of eggs by many marine fishes is associated with

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Table 2. Incidence of three categories of maximal proportional decline experienced by populations of fishes during periods of 15 and 20 years (iteroparous marine and freshwater fishes) and three generations (semelparous salmonids).

		Proportional decline in mature fish biomass–abundance					
	Period of decline	0–49%		50–79%		≥80%	
		n	%	*n*	%	*n*	%
Marine fishes	15 years	59	36.2	55	33.7	49	30.1
	20 years	33	36.3	31	34.1	27	29.7
Semelparous salmonids	3 generations	28	26.5	38	35.8	40	37.7
Freshwater fishes	15 years	7	50.0	4	28.6	3	21.4
	20 years	3	37.5	2	25.0	3	37.5

increased productivity and with increased probability of producing unusually high levels of recruitment.

The ghost, who appeared before Lamarck in the early 19th century (Roberts and Hawkins 1999), was manifested by Thomas Huxley's famous utterance at the Great International Fisheries Exhibition in London in 1883 (see Smith 1994 for historical context), when Charles Darwin's confidant argued,

> That the cod fishery, the herring fishery, the pilchard fishery, the mackerel fishery, and probably all the great sea-fisheries, are inexhaustible; that is to say that nothing we do seriously affects the number of fish.

Huxley was overwhelmed by the vast numbers of eggs that marine fish produce, suggesting to his audience that this great reproductive potential would prevent fishing from having any significant impact on marine-fish stocks. Echoes of this refrain can be heard today, albeit in somewhat modified forms: the great fecundity of marine fishes renders them more resistant to overexploitation and better able to recover after being reduced to small population sizes than fish with more modest egg productivity (e.g., Cushing and Harris 1973; Mace and Sissenwine 1993; Malakoff 1997).

But this refrain is fundamentally flawed, in part because it obfuscates the fact that fecundity is but one of many characters that influence fitness. For example, as discussed by Hutchings (2000*a*), the porbeagle's (*Lamna nasus*) strategy of producing from one to five offspring every year for perhaps 10 or 15 years is equivalent, evolutionarily, to the Atlantic cod's strategy of producing several hundred thousand to a few million eggs every year for perhaps 5–10 years. The result of both strategies is replacement at equilibrium. Intuitively, then, the high fecundity of marine fishes need not imply greater productivity or reduced susceptibility to extinction (Carlton et al. 1999). Indeed, based on their examination of 266 stocks (including 80 species), R.A. Myers and J.A. Hutchings (unpublished data) could find no evidence that fecundity was positively associated with maximum reproductive rate, a reasonable proxy for resistance to extinction and a metric of productivity at low population size.

The theoretical constructs of this argument appear to be borne out by other empirical analyses. Mertz and Myers (1996) could find no association between fecundity and variance in reproductive rate among 36 species of marine fishes (including elasmobranchs, clupeids, gadids, scombrids, and pleuronectids), and a comparison of phylogenetically unrelated marine-fish taxa by Rickman et al. (2000) also suggests that, in general, species with high fecundity are no more likely to produce unusually high levels of recruitment than those with relatively low fecundity.

Furthermore, variance in maximum reproductive rate, r, does not appear to differ between marine and anadromous fishes. Mertz and Myers (1996) estimated variance in reproductive rate as the standard deviation of the natural log of recruitment residuals from a Ricker stock–recruitment model, that is, $\sigma_{\ln R}$. Among 36 marine fishes, $\sigma_{\ln R}$ ranged from ~0.2 for Peruvian hake (*Merluccius gayi*) and Greenland halibut (*Reinhardtius hippoglossoides*) to ~1.35 for chub mackerel (*Scomber japonicus*), a range similar to that observed among five anadromous species, for which $\sigma_{\ln R}$ ranged from 0.3 for Atlantic salmon (*Salmo salar*) to ~1.0 for pink salmon (*Oncorhynchus gorbuscha*). Thus, at low population sizes, marine fishes appear no more likely to produce unusually high numbers of offspring than nonmarine fishes.

Perception: marine fishes are more resilient and have intrinsically faster recovery rates than other taxa

Using the aforementioned fisheries database (Myers et al. 1995*b*), I recorded the largest 15-year percentage decline in mature-fish biomass experienced by each iteroparous marine and freshwater stock, the greatest three-generation population reduction by each semelparous salmonid population, and subsequent population sizes 5, 10, and 15 years (one, two, and three generations for the salmonids) thereafter. The 15-year interval was considered short enough to obtain a reasonably large sample of populations and long enough to be biologically meaningful, approximating the arbitrary three generation time period used to assess risk criterion A (Table 1) by IUCN and COSEWIC (Campbell 1996; IUCN 1999). Marine stocks were represented primarily by six families: Clupeidae (e.g., herring; sprat, *Sprattus sprattus*), Gadidae (e.g., cod, haddock), Scombridae (e.g., mackerel, *Scomber* spp.; tuna, *Thunnus* spp.), Sparidae (e.g., snapper, *Pagrus* spp.), Scorpaenidae (e.g., redfish, *Sebastes* spp.), and Pleuronectidae (e.g., plaice, *Pleuronectes* spp.; Greenland halibut). Semelparous salmonids were represented primarily by pink and sockeye (*O. nerka*) salmon, although some data were also available for chum (*O. keta*), coho (*O. kisutch*), and chinook (*O. tshawytscha*) salmon. The few freshwater species for which data were available for a minimum of 20 consecutive years (15 years for decline plus 5 years for recovery) included yellow perch, *Perca flavescens*; northern pike, *Esox lucius*; walleye, *Stizostedion vitreum*; and blue pike, *Stizostedion vitreum glaucum*.

As described by Hutchings (2000*b*), any increase following a decline in population size, N, could be interpreted as some sort of recovery. For example, recovery t years after a 15-year decline can be determined from a plot of N_{t+15}/N_0 on the ordinate against magnitude of population decline on the abscissa, that is, $1 - N_{t+15}/N_0$. On such a plot, populations exhibiting no recovery would fall on a straight line with a slope of −1 extending from (0,1) to (1,0). Populations continuing to decline would fall below this line, whereas those

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exhibiting some recovery would lie between this line and the full-recovery line (at which $N_{t+15} = N_0$) with a slope of 0 extending from (0,1) to (1,1) (Fig. 1).

Future population size is negatively correlated with magnitude of population decline for both marine and nonmarine fishes. Among 90 marine-fish stocks (38 species, 11 families), 15-year declines ranging from 13 to 99% were followed by 5-year changes to population sizes of 0.3–178% of the sizes from which the declines began, that is, N_0 (Hutchings 2000*b*; Fig. 1*a*). The negative association between 5 year recovery population size and population decline was stronger when clupeids were excluded from the analysis (Table 3). Data 10 and 15 years subsequent to the 15-year population declines were available for 45 and 25 marine stocks, respectively, being composed primarily of clupeids and gadids. Among all stocks, the magnitude of decline negatively influenced population size 10 years, but not 15 years (Fig. 1*b*), after the declines. However, when clupeid data were excluded, population decline was strongly and significantly associated with both 10 and 15 year recovery population sizes (Table 3).

Within families, population recoveries after 5 years were significantly correlated with population declines in gadids, sparids, scorpaenids, and pleuronectids (Table 3; Hutchings 2000*b*). The association was not significant within clupeids or scombrids, although the correlation was highly significant within the latter family when the outlier stock (eastern Pacific yellowfin tuna, *Thunnus albacares*) was removed from the analysis. At the family level, 15 year recovery population sizes were negatively associated with population decline within gadids but not within clupeids (Fig. 1*b*; Hutchings 2000*b*).

For the 86 stocks of semelparous salmonids and seven populations of iteroparous freshwater fishes, the largest three-generation or 15-year decline experienced by each was negatively associated with population size one generation and 5 years thereafter (Table 3; Fig. 2). Within species, the same was true for pink and sockeye salmon (Fig. 3). However, unlike marine fishes, the population sizes of semelparous salmonids were independent of the magnitude of population declines two and three generations after the declines had occurred (Fig. 4). Within species, excluding the outlier (Sunday Creek, Cook Inlet, Alaska; Fig. 3*b*), population sizes of pink salmon three generations after their maximum three-generation declines were negatively associated with the latter ($r = -0.58$, $p = 0.002$).

At the very least, population resilience appears similar for marine and nonmarine fishes, if not actually lower among marine fishes, based on linear regressions between population recovery and population decline (Table 3). For example, 5 years or one generation after experiencing 15-year or 3-generation declines of 80%, populations are predicted to recover to 34% (all marine fishes; 29% if clupeids are excluded), 56% (semelparous salmonids), and 17% (freshwater fishes) of the sizes from which the population declines began. Three generations after a three-generation decline of 80%, pink salmon (excluding the single outlier) are expected to recover to 75% of their population maxima during their declines, compared with only 20%—effectively no change at all—for gadids 15 years after 15-year declines of 80%.

A second comparison of marine and anadromous populations also suggests that the latter may be more likely to recover from collapse than the former. As described above, the broken and solid lines in Figs. 1–4 can be used to identify populations that recover fully (lie above the dashed line) and those that decline further (fall below the solid line) after experiencing their greatest 15-year or 3-generation percentage decline in spawner abundance or biomass. The incidence of full recovery among anadromous populations for the range of recovery periods considered here was more than twice that of marine fishes (Table 4). Similarly, further decline was twice as probable among marine fishes than among anadromous fishes.

Among marine fishes, population-recovery and -decline data suggest that, following prolonged decline, clupeids are more likely to recover to previously experienced population sizes and are more resilient than other marine fishes (Fig. 1; Table 3). As argued elsewhere (Hutchings 2000*b*), such an increased rate of recovery may be attributable to the comparatively younger age at which clupeids mature (Froese and Pauly 1999) and the higher intrinsic rate of increase that earlier maturity generally effects (Roff 1992). Higher reproductive rates are also expected to mitigate the negative influence of environmental stochasticity on the persistence of populations at small sizes (Lande 1993). Earlier age at maturity may also account for the observation that anadromous fishes appear more likely to recover from collapse than marine fishes.

However, the apparent increased resilience evident among clupeids may also be a consequence of differential species selectivities of fishing gear. Clupeids are typically fished by deploying purse seines or midwater trawls. Low species diversity within clupeid schools results in bycatch levels of from one to two orders of magnitude lower than the bottom-deployed seines and trawls used to catch groundfish (Alverson et al. 1994). Thus, when a clupeid stock collapses, it may be comparatively easy to eliminate fishing mortality on the affected population, because of the high species selectivity of clupeid fishing technology. By comparison, the collapse of a groundfish stock rarely results in cessation of bottom trawling in the affected region, meaning that fishing mortality on the collapsed stock can be reduced but rarely eliminated, because of the comparatively low species selectivity of the fishing gear used to capture a broad diversity of demersal marine fishes. In addition to the proposed influence of age at maturity, reproductive rate, and fishing-gear selectivity on recovery rates, it is highly probable that ecosystem-level consequences of exploitation—for example, alterations in food webs effected by changes to species community structure—also play a significant role (Pauly et al. 1997; Jennings and Kaiser 1998).

Thus, with the possible exception of some (but clearly not all) clupeids, there is little empirical support for the perception that marine fishes are more likely than nonmarine fishes to recover from prolonged reductions in abundance. Ideally, of course, it would be preferable to restrict such an analysis of population recovery to those stocks for which fishing mortality post collapse was zero. Unfortunately, such a determination is problematic, because of the difficulty in assessing the degree to which management targets, such as that of attaining a fishing mortality of zero, are met in reality.

From a broader perspective, to what extent might fishes be

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Fig. 1. Bivariate associations between population recovery and population decline for marine fishes. Recovery refers to the size of a population 5 years after the proportionately largest 15-year decline experienced by that population, relative to the size of that population at the beginning of its 15-year decline. Populations that experienced some recovery are represented by points above the solid line. Fully recovered populations are represented by points on or above the dashed line. Each point represents a different marine-fish stock. Data are shown for all stocks (*a*) 5 years and (*b*) 15 years after their greatest 15-year population decline. Families and species represented here include: △, Clupeidae (Atlantic menhaden, *Brevoortia tyrannus*; herring, *Clupea harengus*; Spanish sardine, *Sardinops sagax*; sprat, *Sprattus sprattus*); ×, Engraulidae (anchovy, *Engraulis encrasicolus*; northern anchovy, *Engraulis mordax*); ▽, Osmeridae (caplin, *Mallotus villosus*); ▲, Gadidae (Atlantic cod, *Gadus morhua*; haddock, *Melanogrammus aeglefinus*; whiting, *Merlangius merlangius*; silver hake, *Merluccius bilinearis*; pollock, *Pollachias virens*; Norway pout, *Trisopterus esmarkii*); ◇, Nototheniidae (icefish, *Notothenia rossii*); ■, Scombridae (chub mackerel, *Scomber japonicus*; king mackerel, *Scomberomorus cavalla*; albacore tuna, *Thunnus alalunga*; yellowfin tuna, *Thunnus albacares*; southern bluefin tuna, *Thunnus maccoyii*; bigeye tuna, *Thunnus obesus*; Atlantic bluefin tuna, *Thunnus thynnus*); ◆, Sparidae (New Zealand snapper, *Pagrus auratus*; yellow sea bream, *Taius tumifrons*); ●, Pleuronectidae (petrale sole, *Eopseta jordani*; American plaice, *Hippoglossoides platessoides*; Pacific halibut, *Hippoglossus stenolepis*; common dab, *Limanda limanda*; longhead dab, *Limanda proposidea*; flounder, *Platichthys flesus*; yellowtail flounder, *Pleuronectes ferrugineus*; plaice, *Pleuronectes platessa*; Greenland halibut, *Reinhardtius hippoglossoides*); ○, Soleidae (sole, *Solea vulgaris*); +, Anoplopomatidae (sablefish, *Anoplopoma fimbria*); *, Scorpaenidae (Pacific ocean perch, *Sebastes alutus*; shortspine thornyhead, *Sebastes alaskanus*; redfish, *Sebastes* spp.). (After Hutchings 2000*b*.)

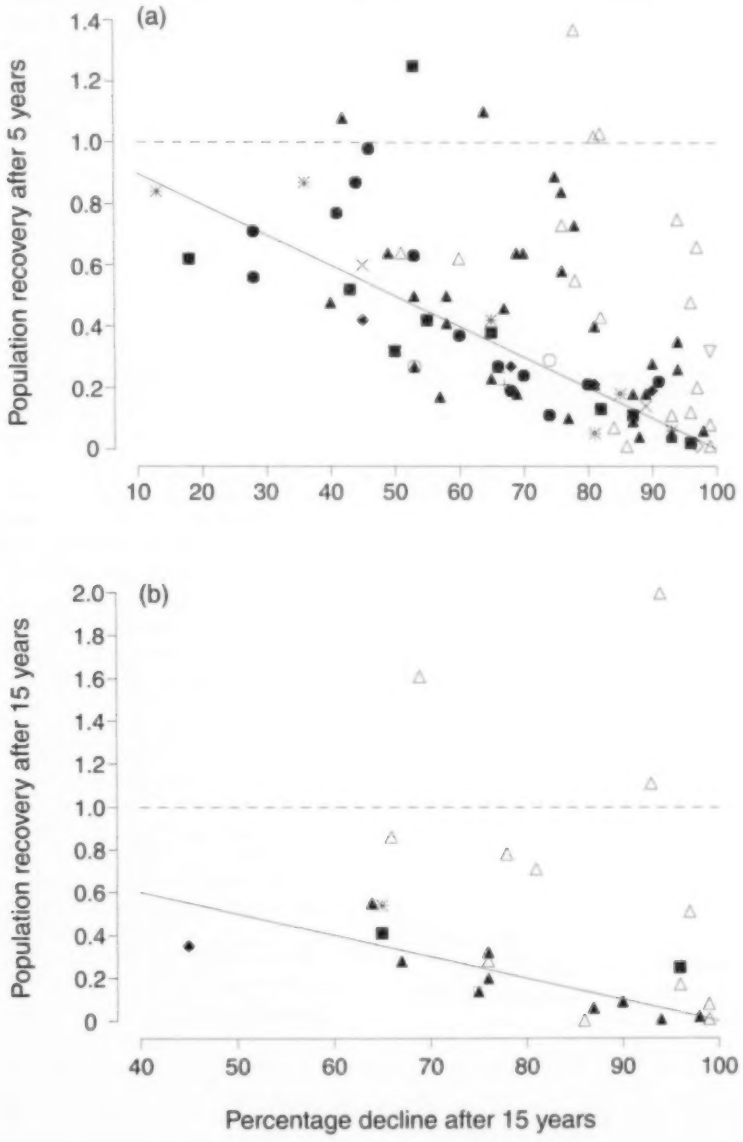

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Table 3. Regression equations describing mature population size (y) after various recovery periods following a 15-year population decline for marine and freshwater fishes, relative to the population size at the beginning of the decline, as a function of population decline (x, percentage decline in mature fish population size over a period of 15 years or three generations).

Recovery period	Taxonomic group	Regression equation	n	p	r
Marine fishes					
5 years	Clupeidae	$y = 1.78 - 1.48x$	20	0.062	–0.42
	Gadidae	$y = 1.14 - 1.00x$	31	0.003	–0.52
	Scombridae	$y = 0.80 - 0.79x$	8	<0.001	–0.96
	Sparidae	$y = 0.65 - 0.53x$	4	0.013	–0.99
	Scorpaenidae	$y = 1.11 - 1.13x$	6	0.004	–0.95
	Pleuronectidae	$y = 1.16 - 1.19x$	13	0.0013	–0.79
	All	$y = 1.00 - 0.82x$	90	<0.0001	–0.46
	All except Clupeidae	$y = 1.04 - 0.94x$	70	<0.0001	–0.64
10 years	Clupeidae	$y = 2.74 - 2.46x$	15	0.083	–0.46
	Gadidae	$y = 1.86 - 1.87x$	16	0.007	–0.65
	All	$y = 1.41 - 1.19x$	45	0.012	–0.37
	All except Clupeidae	$y = 1.46 - 1.42x$	30	0.001	–0.56
15 years	Clupeidae	$y = 3.01 - 2.47x$	12	0.33	–0.32
	Gadidae	$y = 1.22 - 1.28x$	9	0.002	–0.88
	All	$y = 1.06 - 0.60x$	25	0.58	–0.12
	All except Clupeidae	$y = 0.91 - 0.87x$	13	0.004	–0.74
Semelparous salmonids					
1 generation	Pink salmon	$y = 1.78 - 1.51x$	48	0.0003	–0.50
	Sockeye salmon	$y = 1.74 - 1.42x$	25	0.009	–0.51
	All	$y = 1.59 - 1.29x$	86	<0.0001	–0.49
2 generations	All	$y = 1.38 - 0.72x$	37	0.42	–0.14
3 generations	All	$y = 2.11 - 1.42x$	26	0.21	–0.26
Freshwater fishes					
5 years	All	$y = 1.07 - 1.12x$	7	0.0007	–0.96

Note: The regression equation for the Scombridae excludes the outlying eastern Pacific yellowfin tuna stock for which the 5 year recovery population size was 1.25 times the maximum during the 15-year decline. Inclusion of this datum yields the following regression for the scombrids: $y = 0.99 - 0.93x$, $p = 0.078$, $r = -0.62$. Sample size (n) is number of stocks or populations.

expected to have greater resilience than other taxa? One means of assessing this is to compare maximum reproductive rates estimated for fish with those estimated for terrestrial mammals, the organisms upon which many of the extinction criteria used by COSEWIC and IUCN were originally based. R.A. Myers and J.A. Hutchings (unpublished data) documented a range in r among 80 fish species (the majority of which are marine) of between 0.02 and 1.50, with most estimates lying between 0.2 and 0.8. Interestingly, these maximum reproductive rates for fish are not dissimilar to those that have been estimated for large terrestrial mammals such as grizzly bear, *Ursus arctos* ($r = 0.33$; McCullough 1992); bighorn sheep, *Ovis canadensis* ($r = 0.38$; McCullough 1992); white-tailed deer, *Odocoileus virginianus* ($r = 1.00$; McCullough 1979); and saiga antelope, *Saiga tatarica* ($r > 1$; McCullough 1992).

Caveat: increased risk of biological extinction is associated with reduced probability of returning to former levels of abundance

Despite their heuristic value, species-status assessments that attempt to reflect extinction risks alone may not be very useful from an ecological, management, or ecosystem perspective. By intellectually and quantitatively focussing such assessments solely on the vulnerability of a species to biological extinction, there is (not surprisingly) an overwhelming tendancy to critically examine the degree to which criteria such as those used by IUCN and COSEWIC (Table 1) reliably assess the likelihood, for any species, that abundance will decline to zero.

This has led to arguments concerning the quantitative basis for such assessments and the biological legitimacy of time-frame estimates within which specific extinction probabilities will purportedly be realised (see criterion E in Table 1). For example, Musick (1999) has suggested that a 70% decline over the longer of 10 years or three generations be the minimum required before a marine-fish species is assigned to any at-risk category. Basing his population-decline thresholds on maximum reproductive rate, Musick (1999) suggests that, for values of r in the ranges of <0.05 (very low productivity), 0.05–0.15 (low), 0.16–0.50 (medium), and >0.50 (high), a marine-fish species would have to decline, over the longer of 10 years or three generations, 70, 85, 95, and 99%, respectively, to be initially flagged as being vulnerable.

The primary difficulty with focussing one's interpretation of risk or threat categories solely on biological extinction is that, no matter how much modelling might be applied to a specific species, we truly do not understand how the multitude of factors that influence the extinction probability for a given population or species interact with one another

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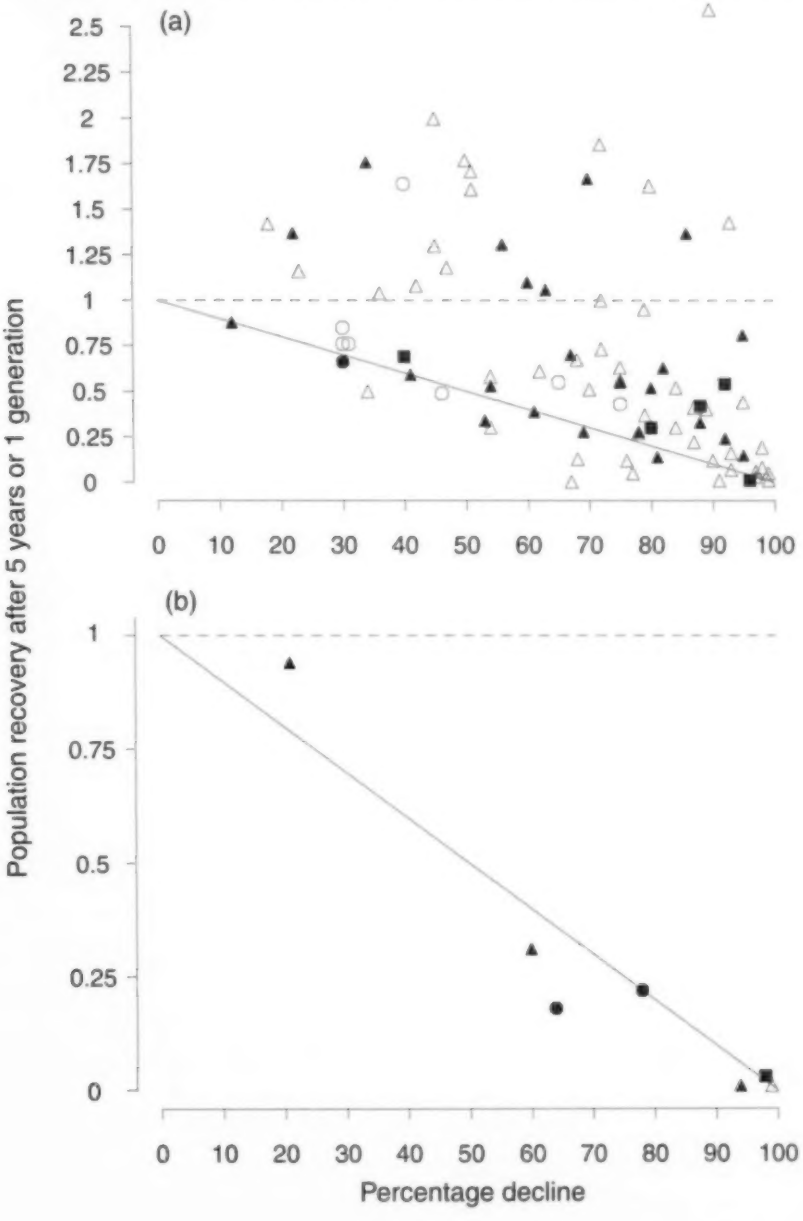
Fig. 2. Bivariate associations between population recovery and population decline for (*a*) semelparous salmonids and (*b*) iteroparous freshwater fishes. Recovery refers to the size of a population one generation (semelparous salmonids) or 5 years (freshwater fishes) after the proportionately largest 3-generation (semelparous salmonids) or 15-year (freshwater fishes) decline experienced by that population, relative to the size of that population at the beginning of its decline. The broken and solid lines represent the "full-recovery" and "no-recovery" lines, respectively. Each point represents a different population. Semelparous salmonids include: △, pink salmon, *Oncorhynchus gorbuscha*; ▲, sockeye salmon, *Oncorhynchus nerka*; ■, coho salmon, *Oncorhynchus kisutch*; ○, chum salmon, *Oncorhynchus keta*; and ●, chinook salmon, *Oncorhynchus tshawytscha*. Iteroparous freshwater species include: ■, yellow perch, *Perca flavescens*; ▲, walleye, *Stizostedion vitreum*; △, blue pike, *Stizostedion vitreum glaucum*; and ●, northern pike, *Esox lucius*.



under specific physical and biological environments. This lack of knowledge, coupled with the absence of an empirical basis upon which to reliably assess quantitative listing criteria, provides a fertile breeding ground for arguments and counterarguments, many of which are based on the perceptions discussed above, concerning the notion that marine fishes should be treated differently from nonmarine fishes, and other taxa, when assigning at-risk status. For example,

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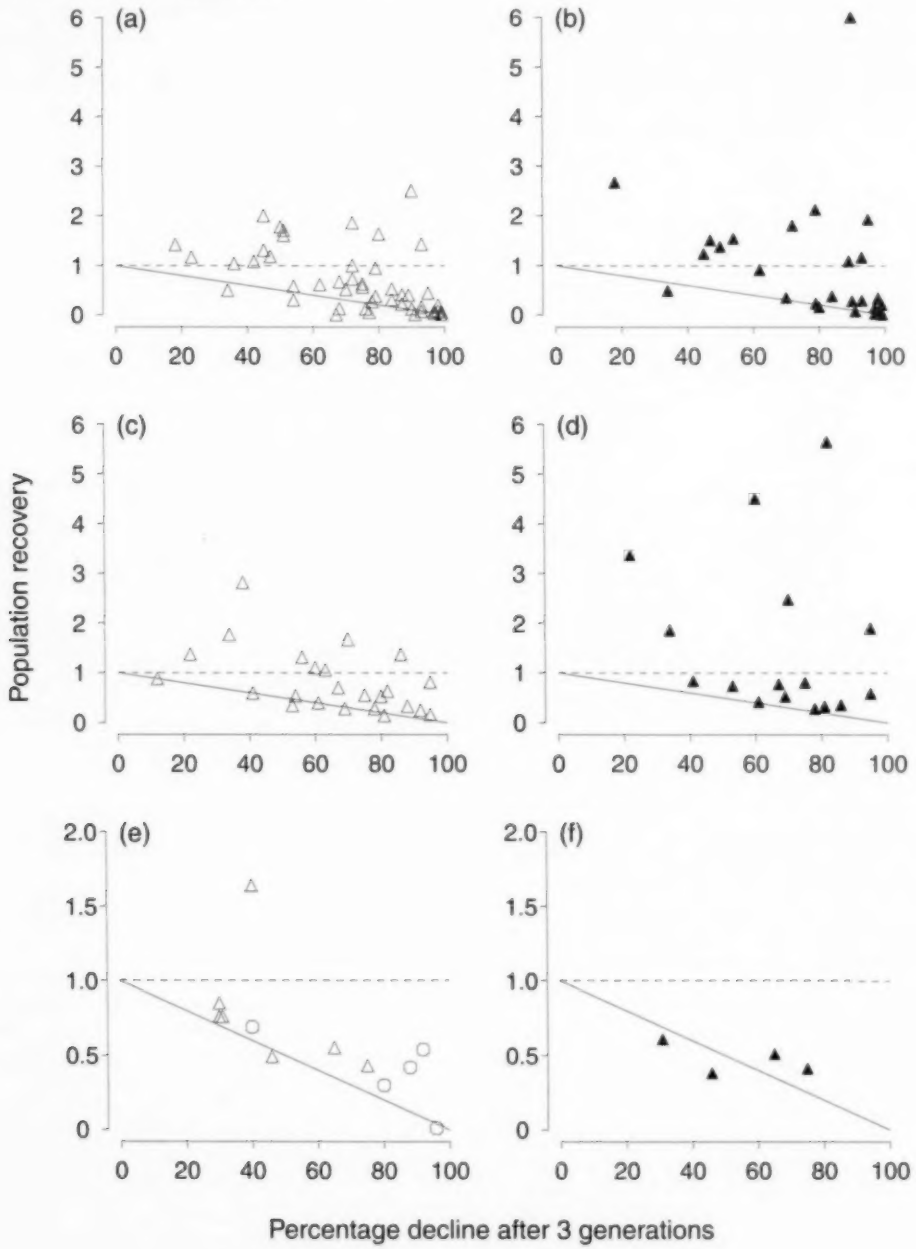
Fig. 3. Population recovery of semelparous salmonids one generation (open symbols) and three generations (solid symbols) after the greatest proportional 3-generation decline experienced by each stock. Data are shown for (*a* and *b*) sockeye salmon, (*c* and *d*) pink salmon, (*e* and *f*; triangles) chum salmon, and (*e*; circles) coho salmon. The broken and solid lines represent the "full-recovery" and "no-recovery" lines, respectively.



one could argue that, even after population declines of more than 95%, most commercially harvested marine fishes would still number in the hundreds of thousands, if not millions, of individuals, and should not be considered at any increased risk of extinction as a consequence. But, again, is it not simply a perception, or an intuition, that such numerical levels should be able to buffer the factors that may conspire to reduce population sizes further, even in the absence of exploitation? For, notwithstanding severe hunting pressures, species abundances numbering in the millions failed to prevent the extinction or extirpation of the passenger pigeon (*Passer domesticus*) or the Eskimo curlew (*Numenius borealis*) in

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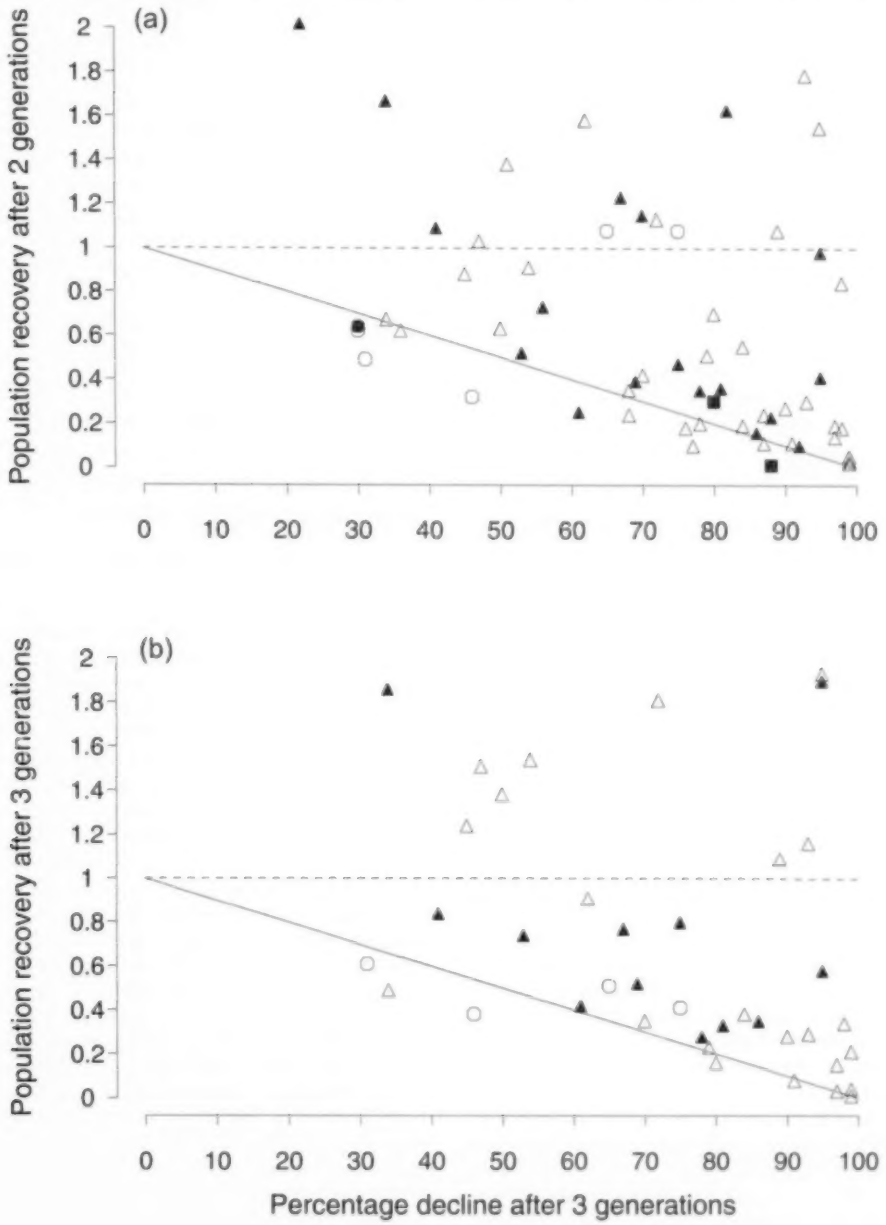
Fig. 4. Population recovery of semelparous salmonids (*a*) two generations and (*b*) three generations after the greatest proportional three-generation decline experienced by each stock. The broken and solid lines represent the "full-recovery" and "no-recovery" lines, respectively. Semelparous salmonids include: △, pink salmon, *Oncorhynchus gorbuscha*; ▲, sockeye salmon, *Oncorhynchus nerka*; ■, coho salmon, *Oncorhynchus kisutch*; ○, chum salmon, *Oncorhynchus keta*; and ●, chinook salmon, *Oncorhynchus tshawytscha*.



North America or, indeed, of marine gastropods in the North Atlantic and North Pacific in the 19th century (Carlton et al. 1999). Certainly, numerical abundance alone was not sufficient to prevent population collapses of Northwest Atlantic cod. And, even in the absence of fishing, numerical abundance alone appears insufficient to ensure recovery to former levels of abundance.

These observations underscore the point that the threat of extinction is a double-edged sword. It reflects not only the probability with which a species' abundance will decline to zero but, just as importantly, the probability with which a numerically depressed species will grow to previous levels of abundance. Northwest Atlantic cod again provide a useful case in point. Deterministic estimates of r for the six Canadian

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Table 4. Incidence (%) of full recovery and further decline among marine and semelparous anadromous fishes 5 years or one generation and 15 years or three generations after the greatest 15-year or 3-generation percentage decline in reproductive biomass or abundance experienced by each population.

	Full recovery		Further decline	
	5 years – 1 generation	15 years – 3 generations	5 years – 1 generations	15 years – 3 generations
Marine fish	7.8 (7)	12.0 (3)	41.1 (37)	40.0 (10)
Semelparous anadromous fish	25.6 (22)	25.6 (10)	22.1 (19)	17.9 (7)

Note: Values in parentheses are sample size (n).

cod stocks to which fishing moratoria were applied in the early 1990s fall within Musick's (1999) medium-productivity category (Myers et al. 1997), although one may be in the low-productivity category (Hutchings 1999). According to Musick's (1999) suggested criteria, these stocks would not have been considered vulnerable until their abundance had declined by at least 95% over the longer of 10 years or three generations. Although only one of these stocks (northern cod; Lilly et al. 1998) declined by this amount, all, with the exception of the stock that had declined least among the six (St. Pierre Bank cod), have failed to return to levels of abundance experienced in the 1980s. So, while there may be no foreseeable risk of biological extinction for these stocks (notwithstanding the potential losses of populations or substocks), there would appear to be a reasonably high probability that these stocks will not return to former levels of abundance.

Assurance that a stock is unlikely to decline to zero surely provides little solace, if that stock has a very low probability of returning, even to a modest extent, to former higher levels of abundance.

Caveat: risk assessments based on abundance trends for single species or stocks may underestimate extinction threats to constituent populations or substocks

Marine fishes typically occupy very broad geographical ranges. As such, many are almost certainly composed of more than one substock or population. This raises the question of whether at-risk designations based upon assessments conducted at the species or stock level are likely to provide risk-averse assessments for substocks within stocks and for populations within species.

Returning to the listing of Atlantic cod by COSEWIC, there was resistance to assigning stocks separately to at-risk categories (Comeau 1998), resulting in a single designation being assigned to the species as a whole in Canadian waters. For, if Atlantic cod are the migratory and evolutionary vagrants that some appear to consider them to be, local groups or substocks can be permitted to go extinct, because cod from other areas will simply fill in the recently vacated waters.

The logical fallacy of this argument lies, of course, in the premise that species, in general, are adapted to colonise new areas. Rather, natural selection tends to select against genotypes that abandon the environments and habitats in which they evolved and to which they have adapted their life histories, spawning times, and migratory behaviour, particularly in the absence of any density-dependent pressure to do so. Not surprisingly, from an ecological perspective, there is increasing evidence of local adaptation within Atlantic cod populations at spatial scales less than those used by management to delineate stocks. Evidence of genetically based population variation includes differences in growth rates (Svasand et al. 1996; Puvanendran and Brown 1998), antifreeze protein levels (Goddard et al. 1999), behavioural responses to photoperiod (Puvanendran and Brown 1998), and spawning time (J.A. Hutchings, unpublished data).

Caveat: reproductive rates differ among populations within species

The use of r as the primary metric for assessing extinction risk is not unreasonable; it is quantitative and has a sound theoretical basis in population and conservation biology. But, in practice, there are at least two reasons why reliance on this metric will be problematic. The first is that r differs among populations within species. Reproductive rate is primarily a product of age at maturity (α) and age- and size-specific rates of survival and fecundity, all of which differ, to greater or lesser degrees, among populations. Within Atlantic cod, one of the best-studied marine fishes from a life-history perspective, age at maturity prior to the commercial fishery collapses of the 1990s ranged between 2 years on Georges Bank and 7–8 years off Norway (Myers et al. 1997). As a consequence of these differences in α, deterministic estimates of maximum reproductive rate vary significantly among cod stocks, ranging at least from 0.17 to 1.15 (Myers et al. 1997; Hutchings 1999).

Returning to Musick's (1999) suggested classification scheme, which deterministic estimate of r would one choose for Atlantic cod? The intrinsic rates of increase for half of the 20 cod stocks examined by Myers et al. (1997) fall within Musick's (1999) high-productivity category ($r > 0.50$), while half fall in the medium-productivity category ($0.15 < r < 0.51$). There is also good reason to believe that r for at least one cod stock falls within the low-productivity ($0.05 < r < 0.16$) category (Hutchings 1999; Shelton and Healey 1999).

In the absence of estimates of the intrinsic rate of increase, Musick (1999) suggested that realised r, estimated at population densities at which density-dependent effects on population growth are likely minimal, might prove a useful substitute. One potential difficulty with this is that realised r will poorly reflect intrinsic r, if the population has experienced changes to age at maturity, individual growth rate, and longevity as a consequence of genetic or phenotypic changes to age at maturity effected by high fishing mortality, reduced

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density, changes to interspecific relationships between predators, prey, and competitors, or some combination thereof.

Thus, species or population assessments are subject to the caveat that intraspecific variation in reproductive rate, or in any fitness-related characteristic, introduces the risk of assigning an inappropriate metric of reproductive rate to a given species or to a specific population within that species. One possible solution to this dilemma when assessing organisms at the species level, as IUCN does, would be to weight r by some metric of virgin-stock size and then to sum across stocks. This may not be an unreasonable approach, providing the number of stocks is small, but the confidence one would have in such a metric would diminish rapidly with increased numbers of stocks, because of the compounding of estimation errors inherent in such a calculation.

Caveat: deterministic estimates of reproductive rate overestimate true reproductive rates

When populations are reduced to very low sizes, their persistence is increasingly threatened by genetic, demographic, and environmental stochasticity (Lande 1993). Among these, environmental stochasticity, defined as unpredictable proportional changes in survival or fecundity that affect all individuals within a population equally, is probably the most important (Caughley 1994).

An attempt to incorporate the effects of environmental stochasticity on estimates of r was made by Hutchings (1999) for northeastern Newfoundland Atlantic cod. He concluded that reductions in age-specific survival as small as 10–20% reduced stochastic estimates of r for this stock from between 0.13 and 0.16 (straddling Musick's medium- and low-productivity categories) to between 0.07 and 0.10. Perhaps more importantly, irrespective of age at maturity or age-specific survival and fecundity, stochastic estimates of r were always less than deterministic estimates (Hutchings 1999).

This almost certainly holds true for all taxa (e.g., red deer; Benton et al. 1995). In general, the stochastic analogue of r in the deterministic model, s, is given by $s = r - \frac{1}{2}(\sigma_s^2)$, where r is the deterministic estimate of the intrinsic growth rate and σ_s^2 is the environmental variance of the intrinsic growth rate (Lande 1993; Lande et al. 1997). Thus, given that environmental influences on age-specific rates of survival and fecundity will never be nil, the true value of r, estimated by its stochastic analogue, will always be less than deterministic estimates of r. The magnitude of the difference between stochastic and deterministic estimates of maximum reproductive rate can be expected to differ among populations and may differ within populations through time. Thus, assessments of extinction risk based on deterministic estimates of r will be, to greater or lesser degrees, risk prone.

Concluding remarks

Contemporary perceptions of the ability of marine fishes to recover from population decline do not have particularly strong theoretical or empirical support. Marine fishes appear to be no more likely to experience reductions in population size than nonmarine fishes. The question of whether natural temporal variability in the reproductive component of marine-fish populations exceeds that of other taxa, including terrestrial mammals and birds, remains a relevant, and to date unexamined, research question. High fecundity is unlikely to provide any insurance against extinction, and available data provide no support for the hypothesis that marine fishes are able to recover rapidly from population collapse (Hutchings 2000*b*).

Based on these observations, I have suggested that to exempt marine fishes from the population-decline criterion used to assign extinction risk would be inconsistent with a precautionary approach to fisheries management and to the conservation of marine biodiversity (Hutchings 2000*b*). This is based, in part, on the argument that increased probability of extinction is logically associated with reduced probability of recovery, and that persistence at relatively low abundance and absence of recovery are scientifically defendable metrics of extinction probability. One could argue that such a conclusion is overly cautious and that "common sense" and "intuition" inform us that marine fishes warrant population-decline thresholds considerably higher than those considered applicable to all other taxa. If so, common sense also dictates that changes to at-risk criteria for marine fishes be based on analyses of empirical data rather than on intuitive perceptions.

Recently proposed decline thresholds for marine fishes, ranging from 70 to 99% over the longer of 10 years or three generations (Musick 1999), may be akin to threading the extinction needle just a little too finely. In any event, the degree to which any criterion adequately reflects extinction probability cannot be known until substantial numbers of species have gone extinct, an obviously undesirable necessity and one that may require considerable amounts of time. So, rather than changing the risk criteria, one could change the names of the risk categories so that they better reflected the goals of conservation and preservation of biodiversity. For example, even if an 80% decline in a cod population does not significantly increase its probability of extinction, it certainly appears to affect its probability of recovery to former levels of abundance. So, irrespective of whether quantitative criteria adequately reflect extinction risk, they do appear to adequately reflect recovery potentials, something of clear importance to resource managers, harvesters, ecologists, and conservation biologists. Rather than having risk categories named vulnerable, threatened, endangered, and critically endangered, one could replace them with conservation categories named priorities I, II, III, and IV.

By disentangling biological extinction probabilities from the process of identifying species and populations of conservation concern, one might eliminate, or at least reduce immensely, the largely unproductive attempts to produce new versions of ultimately imprecise extinction threat criteria. Such a change would also acknowledge that factors such as recovery potential are integral to, and not disassociated from, the process of evaluating extinction probabilities. The most compelling argument against such a name change, and the reason why IUCN and other organisations use extinction risk rather that another measure, such as recovery probability, is that the word "extinction" is more emotive and more readily grabs the attention of the public and decision-makers than does "recovery."

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It needs to be reiterated that, rather than quantifying extinction probabilities, the IUCN and COSEWIC criteria are only guidelines for assigning species to various at-risk categories, each of which *heuristically* reflects extinction probabilities, based on comparatively recent negative changes to a species' distribution and abundance. The primary value of assigning a given species, or population, to one of these categories lies in its conveyance to scientists, to resource managers, to politicians, and to society that a species' extinction probability has increased and (or) that its probability of recovering to some historically high benchmark of abundance is low. It behooves us as scientists not only to recognise the extraordinary value inherent in communicating such a message, but to objectively assign species to at-risk categories independently of managerial, governmental, or political considerations (Hutchings et al. 1997; Leiss 2000).

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"Essential fatty acids" in aquatic ecosystems: a crucial link between diet and human health and evolution[1]

Michael T. Arts, Robert G. Ackman, and Bruce J. Holub

Abstract: Fatty acids (FA) are inextricably linked with key physiological and biochemical processes and are thus integral to proper ecosystem functioning. FA not biosynthesized effectively by animals are termed essential fatty acids (EFA). These EFA are important "drivers" of ecosystem health/stability and are therefore highly conserved in aquatic food chains. Aquatic organisms have been and continue to be our primary source of readily available EFA. However, overfishing and our burgeoning population may be acting in concert to threaten our access to this source of EFA. Here, we review the marine FA synthesis/transport cycle and traditional and nontraditional sources of EFA. Our review suggests that, while some traditional sources of marine oils (e.g., tuna) are in steady decline, other sources (e.g., krill) and technologies (e.g., heterotrophic fermentation) hold great promise for maintaining our access to EFA. We provide a minireview which illustrates that EFA contribute to our health and well-being. Finally, there is growing evidence that EFA have been an important force in our past evolution, leading us and others to speculate that an unbroken link exists between EFA, our present health, and, in all likelihood, our continuing evolution.

Résumé : Les acides gras (FA) sont intimement liés aux mécanismes physiologiques et biochimiques essentiels et sont donc nécessaires au bon fonctionnement des écosystèmes. Les FA non biosynthétisés efficacement par les animaux sont dits des acides gras essentiels (EFA). Ces EFA sont d'importants moteurs de la santé/stabilité des écosystèmes et c'est pourquoi ils sont fortement conservés dans les chaînes alimentaires aquatiques. Les organismes aquatiques ont été et continuent d'être notre source principale d'EFA facilement accessibles. Cependant, l'effet combiné de la surpêche et de l'accroissement de la population humaine pourrait mettre en péril notre accès à cette source d'EFA. On trouvera ici une revue des cycles marins de synthèse et de transport des EFA, ainsi que des sources traditionnelles et inusitées de ces acides gras. Bien que certaines sources traditionnelles d'huiles marines (e.g., le thon) soient en déclin continu, d'autres sources (e.g., le krill) et certaines technologies (e.g., la fermentation hétérotrophe) semblent prometteuses pour maintenir notre accès aux EFA. Les effets positifs des EFA sur notre santé et notre bien-être sont brièvement mis en lumière. Il y a, enfin, des indices de plus en plus convaincants que les EFA ont joué un rôle important au cours de notre évolution; cela nous amène, comme d'autres avant nous, à faire l'hypothèse qu'il existe un lien ininterrompu entre les EFA et notre santé actuelle et vraisemblablement aussi, avec la poursuite de notre évolution.

[Traduit par la Rédaction]

Introduction

As we enter this next millennium, we face profound, multifaceted challenges. One of the most urgent is ensuring that we can secure foodstuffs not only in adequate quantity, but also of high quality. Modern nutritional theory, for example, is focusing our attention on the numerous health benefits of maintaining sufficient levels of fatty acids (FA) and, in particular, preformed long-chain (i.e., C_{20} and C_{22}) polyunsaturated fatty acids (PUFA) in our diets. Marine fish/shellfish remain the principal source of these PUFA (Ackman 1988; Thomas and Holub 1994). Fish/shellfish stocks, however, are in decline worldwide (Williams 1998). Furthermore, new evidence suggests that we are, in effect, "fishing down" our marine food webs, i.e., the mean trophic levels of catches are in decline in several important fisheries (Pauly et al. 1998). Simultaneously, the United Nations estimates that the current world population is nearly 6 billion humans and could reach 8.9 billion by 2050 AD. The dilemma here is that an ever-increasing human population and technological advances in fish harvesting have merged to severely reduce some populations of the most desirable (in terms of FA composition) of the highest trophic level fish species. What are the implications of these two opposing trends in terms of our

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access to these PUFA? Are there alternative, viable sources of PUFA? How important are these compounds to human health and evolution (see Acknowledgments for an expanded definition of the term evolution)?

Here, we explore the fundamental link between ecology and human nutrition within the context of essential fatty acids (EFA). We briefly summarize the pros and cons involved with sourcing, production, and blending of various oils, highlighting some of the more viable alternative sources of EFA. We also provide new information on FA profiles in amphipods from prairie ponds and demonstrate that these organisms are relatively rich in two EFA. In order to clearly establish the requirements and benefits of these compounds, we provide a minireview of the effects of EFA on human health. We conclude with a discussion of the possible role of EFA in human evolution.

Terminology: essential fatty acids

Some FA are considered to be EFA in that they cannot be biosynthesized with an efficiency sufficient to meet our needs. The irony is that α-linolenic acid (ALA, C18:3ω3[3]) and linoleic acid (LA, C18:2ω6) are still called the only "essential" FA by most nutritionists and some biochemists. This term was coined in the 1930s in studies with rats and it has been a long and hard road to persuade scientists that it is the longer-chain C_{20} and C_{22} successor PUFA that are of vital concern to the functioning of most of the organs of our bodies (Holman 1998). Cunnane (1996) argued, on the basis of modern nutritional studies, that the term "essential fatty acid" is outdated when applied to ALA and LA, the precursors of eicosapentaenoic acid (EPA; C20:5ω3) + docosahexaenoic acid (DHA, C22:6ω3) and arachidonic acid (ARA, C20:4ω6), respectively. Instead, he recommended that the term "conditionally dispensable" be used in reference to LA and ALA. This recommendation is based on the observations that we have (*i*) an innate ability to synthesize ALA and LA from C_{16} PUFA precursors present in our diets, (*ii*) imprecise knowledge of true LA requirements, and (*iii*) an absence of clear symptoms of LA and ALA deficiency in healthy adults (Cunnane 1996).

Although some research (Carnielli et al. 1996; Salem et al. 1996) has demonstrated qualitatively that humans can convert the parent ALA to EPA and then to DHA, the most recent consensus is that the degree of conversion is "unreliable and restricted" (Gerster 1998). Furthermore, the rates of conversion (determined with ^{13}C-labeled precursors) suggest that, with a background diet high in saturated fat, conversion of ALA to long-chain metabolites is only ~6% for EPA and 3.8% for DHA in adults (see Gerster 1998 and references therein). In support of this, Emken et al. (1994) estimated a similar conversion efficiency of ALA to DHA in adults of ~5%. Furthermore, with a diet rich in ω6 PUFA, these conversion rates may be reduced by as much as 40–50% (Gerster 1998). On this basis and after examination of the available epidemiological studies showing an inverse association between cardiovascular disease (CVD) and fish consumption, the British Nutrition Foundation has officially recommended a diet including two or three portions of fatty fish per week (equivalent to 3–4 g standardized fish oil·day^{-1}) or, more specifically, 1.25 g EPA+DHA·day^{-1} (Gerster 1998). Similarly, Simopoulos et al. (1999) indicated that 0.65 g·day^{-1} corresponds to an adequate intake of EPA+DHA. We therefore here restrict our definition of the phrase "essential fatty acids" to mean preformed long-chain fatty acids (i.e., EPA and DHA) that cannot be synthesized in sufficient quantity to insure optimal physiological performance. That is, ideally, adequate amounts of EFA should be available for the best possible level of neural development (especially in infants) and, during adulthood, for the prevention and mitigation of cardiovascular, inflammatory, and other diseases (see below).

Marine fatty acid biosynthesis/transport cycle

In marine plants, the proportion of FA in lipids is only 40–50% by weight. This is because the total includes a large non-FA (carbohydrate) component composed of galactolipids (an often neglected part of total algal lipids; Parrish et al. 1992). If one assumes that the North Sea phytoplankton community structure is similar to that of the phytoplankton community off the coast of Nova Scotia, then their FA content would be 0.5–0.8% as wet weight (Ackman et al. 1968). The 530×10^6 t of North Sea photosynthetic biomass (Christensen 1977) could then accumulate only 0.25×10^6 t of FA.

The whole-body fat concentration of noncommercial Nova Scotian fish such as American sand lance (*Ammodytes americanus*) is 6–8% (Ackman and Eaton 1971). They are a major prey item for local Atlantic cod (*Gadus morhua*). The latter are identical to North Sea Atlantic cod and have a variable total fat content (Jangaard et al. 1967), but if it is taken as typically 5% of body weight, the 5×10^6 t of North Sea Atlantic cod would contain ~0.25×10^6 t of FA.

These figures create an apparent paradox. Removal of a small proportion of fish near or at the top of the food chain appears to remove the total year's production of FA. The explanation is, of course, that there is a tremendous buffer of lipid "tied up" in all the trophic levels in the oceans, but only the PUFA are conserved by animals at all trophic levels. They are a component of membrane phospholipids, transmit neural signals, are crucial for vision, and control ionic balance including gill function. Further, the very low melting points (approaching –50°C) of long-chain PUFA (LCPUFA) in their free form means that they will also remain highly fluid in situ and thus play an important role in biochemical adaptation to cold environments in aquatic ectotherms.

The transfer of FA from plants to higher animals is very uneven and must therefore be considered in terms of bioconcentration. For example, as noted above, primary productivity in the North Sea yielded ~530×10^6 t of biomass in 1970. Zooplankton and benthic invertebrates converted this to an estimated 41×10^6 and 55×10^6 t of biomass, respec-

[3] In the lipid shorthand commonly in use today, *m*:*p*ω*x* and *m*:*pn*–*x* are identical notations for a fatty acid with *m* carbon atoms, *p* ethylenic bonds (methylene interrupted if more than one), and *x* carbon atoms from and including the terminal methyl group to and including the carbon atom of the nearest ethylenic bond.

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Table 1. Distribution of selected FA (% wet weight) in various marine organisms compared with Atlantic menhaden oil.

		Animal tissues (whole)			
Component	Atlantic menhaden oil[a]	Common oyster (*Crassostrea virginica*)[b]	Northern krill (*Meganyctiphanes norvegica*)[c]	Atlantic salmon[d]	Skipjack tuna[e]
C14:0	7.3	3.5	4.6	5.5	–8.2
C16:0	19	25.9	18.4	10.2	26.5
C18:0	4.2	3.6	2.2	2.7	11.9
ΣSAFA	30.5	36	25.2	18.4	>38.4
C16:1	9.1	4.2	3.5	8.1	–8.2
C18:1	13.2	8.2	14.7	16.9	6.8
C20:1	2	5	2.3	15.1	0.5
C22:1	0.6	0.3	0.9	14.4	—
ΣMUFA	24.9	17.7	21.4	54.5	>7.3
C18:2ω6	1.3	2	1.8	4.5	1.1
C18:3ω3	1.3	3.3	1.3	0.9	0
C18:4ω3	2.8	2.6	3.1	1.7	1.3
C20:4ω6	0.2	2.3	1	0.6	3.1
C20:5ω3	11	11.2	10.8	6.2	11.1
C22:5ω3	1.9	—	1	1.8	—
C22:6ω3	9.1	9.7	28.6	9.1	29.1
ΣPUFA	27.6	31.1	45.8	24.8	45.7
Other	17	15.2	7.6	2.3	—

[a]Ackman (1982).
[b]Watanabe and Ackman (1974).
[c]Mayzaud et al. (1999).
[d]Aursand et al. (1994).
[e]Tanabe et al. (1999). Data for juveniles (0.19–0.25 g). Analyses were by high-pressure liquid chromatography, therefore 14:0 and 16:1ω7 were not separated.

tively. Some was consumed by other successful and stable fish populations involved, such as sand lances (*Ammodytes* sp.), that contribute to the diet of Atlantic cod and other gadoids (Ackman et al. 1986), but only 5×10^6 t of Atlantic cod and similar commercial fish could live off this level. The crux of the matter is that, from an FA perspective, $\leq 3 \times 10^6$ t of Atlantic cod could be harvested annually in a sustainable fishery.

Saturated FA (SAFA) and the most common monounsaturated FA (MUFA) (C16:1ω7, C18:1ω9, C18:1ω7) can be biosynthesized de novo by most animals. Algal polysaccharides may be used as raw material for this purpose in lower trophic levels either through grazing or through direct intake of marine colloids (Liu et al. 1998). These polysaccharides are a basic part of detritus and seston layers (Parrish et al. 1995) and serve as bacterial substrates. As far as we know, this component of FA biosynthesis has never been seriously considered despite the vast quantities of available plant polysaccharides.

Atlantic menhaden (*Brevoortia tyrannus*) are a good example of direct transfer of FA from primary producers to fish. Adult Atlantic menhaden are filter-feeders that produce an oil with roughly one third each of SAFA, MUFA, and PUFA (Table 1; Fig. 1). The unicellular alga *Chaetoceros calcitrans* is a typical food item of Atlantic menhaden and is also widely used in shellfish nutrition research. It has a relatively simple FA composition, although the family of C16:2ω4, C16:3ω4, and C16:4ω1 FA (Fig. 1) is not commonly encountered by lipid chemists. Green algae tend to produce relatively simple FA mixtures based on C_{18} PUFAs (Volkman et al. 1989). Even so, the metabolism of FA by Atlantic menhaden, possibly aided by gut bacterial action, produces a variety of branched-chain FA, odd-numbered FA, and a few extra isomers of PUFA such as C20:4ω3 (Ackman 1989). This accounts for the numerous extra peaks in the chromatogram (Fig. 1).

The FA selected for presentation are usually rather limited, even though, since the early 1970s, over 60 FA can be found with capillary (open-tubular) gas–liquid chromatography. Figure 2 shows some well-known ones, but the choice of FA presented in Tables 1 and 2 is based on nine that are likely to be quantitatively important and three (C18:2ω6, C18:3ω3, C20:4ω6) that are of nutritional interest in fish oils or meals used in animal feeds. If one discounts C20:1 and C22:1, there is only one generic cold-water marine fish oil (based on triacylglycerols) similar in composition to Atlantic menhaden oil (Ackman et al. 1988). The phytoplankton in the diet of Atlantic menhaden do not contain C20:1 and C22:1, and consequently, they are barely present (1–2%) in that fish's oil. Those two FA are derived principally from fatty alcohols of copepod wax esters where the dominant C22:1 alcohol isomer is C22:1ω11 (Sargent 1989). This C22:1 structure transfers to most common North Atlantic fish body oils such as capelin (*Mallotus villosus*), Atlantic herring (*Clupea harengus*), and Atlantic mackerel (*Scomber scombrus*) where low levels of the free fatty alcohols C16:0, C18:1, C20:1, and C22:1 can all be found, obviously having escaped the hydrolysis and oxidation processes in the gut wall that convert most of the alcohol of wax esters to the corresponding FA (Ratnayake and Ackman 1979*a*, 1979*b*). The copepods may produce this unusual C22:1ω11 isomer to maximize the buoyancy effect of their wax esters. Copepods

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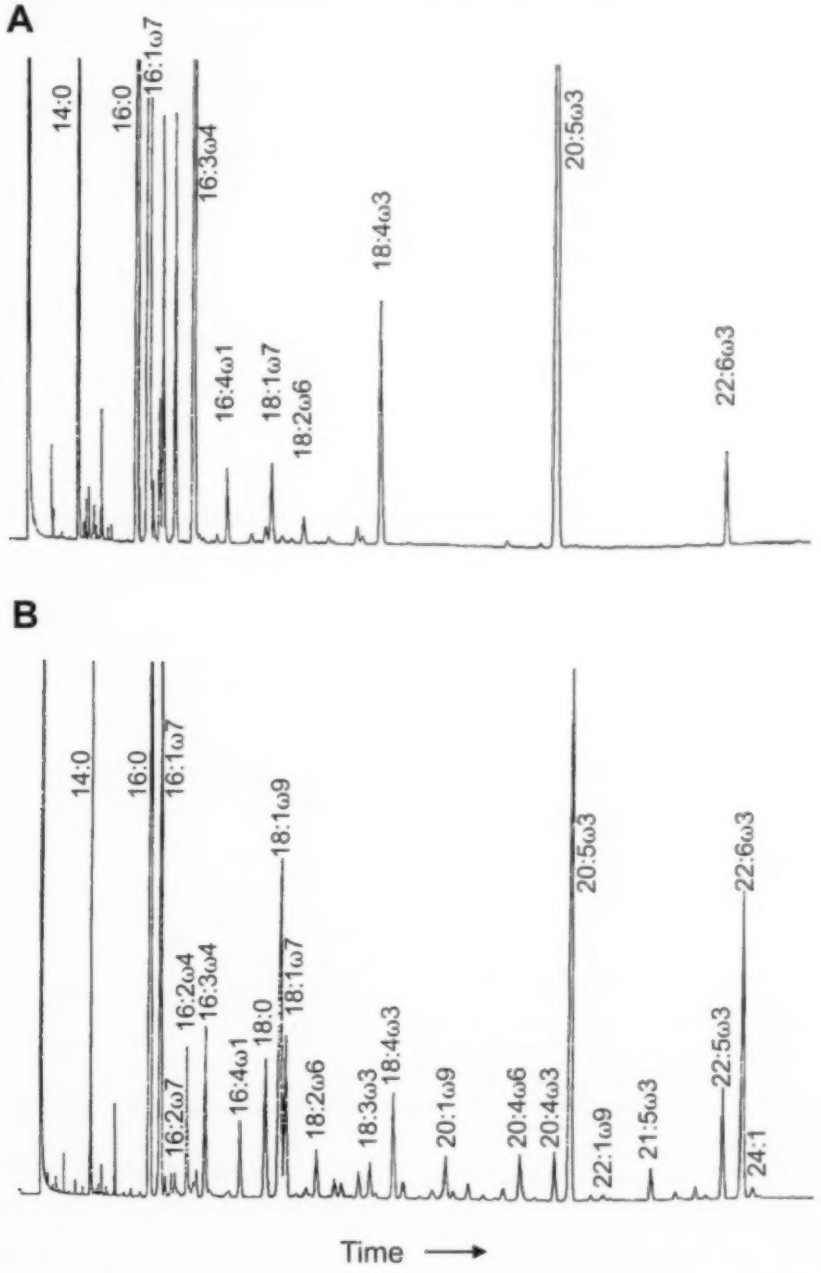
Fig. 1. Gas–liquid chromatograms showing representative FA of (A) the marine phytoplankter *C. calcitrans* and (B) the typical fish oil of Atlantic menhaden. Adapted from a figure first presented in Ackman and Kean-Howie (1995).



are the main component of the trophic level that converts plant material to animal material. This large-scale production of copepod-derived C22:1ω11 results in the dominance of this isomer in the C22:1 group of fish depot fats right up to seals and even circulates in humans eating seal fat (Ackman et al. 1980), although usually accompanied by C22:1ω13, C22:1ω9, and C22:1ω7.

In fish, depot triacylglycerols and flesh phospholipids typically contain ~95 and ~75% FA by weight, respectively. A review of fish triacylglycerols demonstrates that only a few of these molecules from any marine fish oil will contain EPA and DHA (Moffat 1995). This occurs because, in the triacylglycerol depot fats of fish, there is a fair degree of specificity in FA assembly (Brockerhoff et al. 1963, 1964).

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Fig. 2. FA likely to be observed in aquatic organisms, including phytoplankton and macrophytes. The notation clearly shows the family relationships between those of different chain lengths (Ackman 1999).

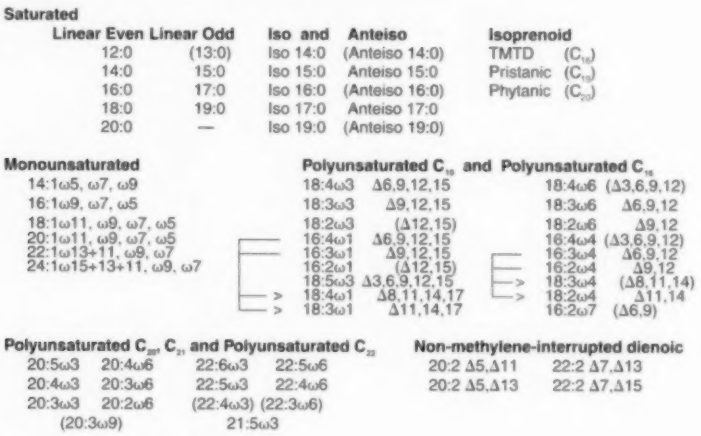

Table 2. FA concentrations (% wet weight) in different body tissues of a North Atlantic squid (*Illex illecebrosus*) compared with two cephalopods and a fish common in South African waters.

Component	Sole (*Solea vulgaris*) flesh[a]	Octopus (*Octopus vulgaris*) flesh[a]	Squid (*Loligo vulgaris*) flesh	*I. illecebrosus*[a]	
				Liver	Flesh
C14:0	4.3	2.7	2.5	4.4	2.2
C16:0	16.2	23.8	24.6	13.7	27.6
C18:0	6.9	10	2.8	1.8	4.4
ΣSAFA	29.2	38.4	30.4	19.9	34.2
C16:1	6.2	0.7	1.5	9	0.4
C18:1ω9	10.7	7.2	4.1	16.3	4.9
C18:1ω7	4	—	1.4	—	—
C20:1	3	3.8	4.6	12.4	4.9
C22:1	1.3	1.7	0.4	8.2	0.5
ΣMUFA	25.7	13.4	12.5	45.9	10.7
C18:2ω6	1.4	—	0.7	0.8	0.3
C18:3ω3	—	—	—	0.4	0.1
C18:4ω3	0.1	—	0.9	0.8	0.1
C20:4ω6	1.7	6.3	1.3	0.4	0.8
C20:4ω3	—	—	0.2	0.4	—
C20:5ω3	7.3	16.1	14.3	13.9	15.8
C22:5ω3	8.7	1.8	0.4	1.3	0.3
C22:6ω3	14.4	20.6	31.6	16.9	37.1
ΣPUFA	36.9	44.8	49.7	34.9	54.5
Other	8.2	3.4	6.5	—	—

[a]Riley (1999).
[b]Jangaard and Ackman (1965).

Specifically, biosynthesis via a phospholipid first stage is directed by enzymes that put a PUFA in the center (*sn*–2) position (Fig. 3). In the last (*sn*–3) position, all FA, including C22:1 and C20:1, derive from whatever FA are in the diet and are circulating in the blood when the triacylglycerol molecules are assembled. Thus, most of the DHA will be located in the central position of phospholipids, with most of the remaining EPA and DHA circulating in the fish's blood (especially after a meal).

There is less C22:1 in Atlantic cod and Atlantic salmon (*Salmo salar*) oils as compared with Atlantic herring, for example, which may contain up to 30% of their FA as C22:1. This reinforces the conclusion that these two fish are at a higher trophic level. Atlantic cod and Atlantic salmon, of course, do not, as adults, eat the C:22:1-rich copepods. Thus, it follows that C20:1 and C22:1 are generally absent in the phospholipid precursors of Atlantic salmon triacyglycerols and therefore that these two FA will also rarely be found in the *sn*–2 and *sn*–3 positions of Atlantic salmon triacylglycerols (Fig. 3). In fact, with the exception of C20:1 and C22:1, the FA composition of several freshwater fish does not differ radically from that of marine fish (Henderson and Tocher 1987). Other freshwater fish such as carp (mostly common carp (*Cyprinus carpio*)), tilapia (Mozambique tilapia

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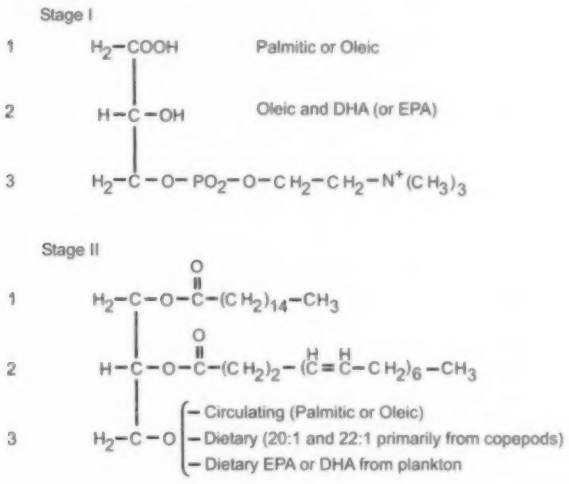
Fig. 3. Biosynthesis of a fish oil triacylglycerol molecule. The first stage is a phospholipid that may have any one of four common FA (myristic, C14:0; palmitic, C16:0; palmitoleic, C16:1ω7; or oleic, C18:1ω9) in the *sn*–1 position. The phospholipids would prefer a highly unsaturated FA (e.g., EPA or DHA) in the *sn*–2 position, but depending on whether the fish is in either the biosynthesis or the catabolism status for energy, the assembly process may have to again use a common FA. Finally, in the last stage of assembly, any of the currently surplus FA (e.g., C20:1, C22:1) from the diet or from the normal blood circulation are inserted.



(*Tilapia mossambica*) or Nile tilapia (*Tilapia nilotica*)), channel catfish (*Ictalurus punctatus*), and similar herbivorous fish are now the subject of intense nutrition research by aquaculturalists.

The Atlantic salmon FA of Table 1 are relatively high in C22:1 because these were farmed fish fed on capelin or Atlantic herring meal and oil. However, Atlantic cod and Atlantic salmon employ a selective deposition or catabolism process so that their oils will contain a little less C22:1 than C20:1 relative to the ratio in the diet. For example, migrating Pacific salmon preferentially use up C22:1 for energy. Other salmonids such as rainbow trout (*Oncorhynchus mykiss*) also selectively use C22:1 as an energy source (Henderson et al. 1982). However, Jezierska et al. (1982) reported that MUFA are utilized first on starvation in rainbow trout.

Sources of essential fatty acids

Aquatic sources

Marine sources of essential fatty acids

Familiar fish species used in the production of fish oil include, among others, anchovies, capelin, Atlantic cod, Atlantic herring, Atlantic mackerel, Atlantic menhaden, salmonids, sardines, shark (liver), and tunas. A recent addition to commercially available marine-sourced oils is seal oil. Seal oil differs from fish oils in that it contains appreciable amounts of docosapentaenoic acid (*n*–3 DPA, C22:5ω3). This form of DPA is valuable in that it is reputed to be at least 10 times more effective than EPA in inducing endothelial cell migration (Kanayasu-Toyoda et al. 1996), a process critical in wound repair and in keeping arteries soft, supple, and clear of deposits. Marine oils are still the least expensive natural source of preformed long-chain PUFA, and several industries (e.g., Ocean Nutrition, Halifax, N.S., Canada, and Pronova Biocare, Sandefjord, Norway) now specialize in their production and purification through cold pressing, further concentration by winterization (i.e., chilling), and other technologies.

There are, however, potential problems associated with fish oils as a source of PUFA. These may include taste, odor, and stability problems as well as the presence of coextracted contaminants. Refining insures that fish oils conform to edible-food standards, and, to a great extent, gelatin encapsulation and deodorization negate the taste and odor issue. Deodorization also reduces organic contaminant levels in fish oils (Hilbert et al. 1998). Volatile components are among the most effectively removed contaminants; however, highly lipophilic contaminants (e.g., dieldrin and some 1,1,1-trichloro-2,2-bis-(*p*-chlorophenyl)ethane (DDT) congeners) may remain at low levels. Clearly, a focus on obtaining source fish from a pristine environment is prudent. Another potential problem with fish oils is that the term is sometimes used generically. That is, "fish oil" can be obtained from a variety of fish species, locations, and seasons, and each of these variables influences the ultimate FA composition of the oil.

Beyond these issues, the concern that fish/shellfish stocks are in worldwide decline signals us to both protect existing EFA sources and be receptive to new sources of EFA. Furthermore, it is not yet cost effective to biochemically synthesize EFA on a commercial scale and we may therefore have to utilize "nontraditional" sources of EFA such as those presented in the following sections.

There is a gradation of desirability for food use among fish resources in the ocean. For example, a plentiful species such as capelin could be further exploited, as there already is a sound meal and oil industry in Iceland and Norway and a limited food industry based on roe only. Capelin is a circumpolar species that, like American sand lance, is an intermediary between zooplankton and the commercially valuable gadoids. There are two North Atlantic populations of special interest. One is heavily fished in Iceland and migrates thence to Norway. There, together with the Barents Sea stock, capelin support a vigorous Atlantic cod stock and are heavily fished for meal and oil. The second population spawns in June–July in Newfoundland and can have a fat content as high as 18% when feeding in waters off Labrador (Eaton et al. 1975). The Japanese consume large amounts of roe, and although some attempts to develop food products for North American tastes have been made (Jangaard 1974), capelin is a typical example of a pelagic fish with high edible potential that is rarely used directly for food. This is unfortunate, as, for unknown reasons, the lipids of frozen capelin are remarkably resistant to oxidation (Botta et al. 1983).

The capelin situation must be contrasted with the vast numbers of Myctophidae, or lanternfishes. These attracted attention among biologists several decades ago because of their diel migrations, midwater habitat, and large numbers (Neighbors and Nafpaktitis 1982). Possibly, diel migrations would allow commercial exploitation, but so far, utilization

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has not been seen as practical because of wax esters discovered in the bodies of several species (Lee and Patton 1989). This, together with their small size, will likely preclude their use as food by humans. Another midwater family, the lightfishes or bristlemouths (Gonostomatidae), have lipids similarly rich in wax esters.

Wax esters are not necessarily all bad, as for example in the case of the orange roughy (*Hoplostethus atlanticus*) from New Zealand. The tissues of this large, deep-dwelling (1000 m) teleost fish were shown to be rich in wax esters (Hayashi and Takagi 1980). Subsequently, a deep skinning technique was developed and the delicious white muscle fillets were a market success in North America. Unfortunately, the fishery soon virtually collapsed, mainly because it was not appreciated that reproduction and replacement rates of this fish are extremely slow. Hopefully the development of fisheries for other edible deepwater fish species with wax esters (e.g., off Australia's coasts Bakes et al. 1995) will learn from this experience.

Tuna are grossly overfished and yet little is known about their early life stages. Juvenile tuna are known to have very high total body contents of EPA and DHA. The total lipid concentrations of skipjack tuna (*Katsuwonus pelamis*) tuna range from 2.24 to 4.0% (wet weight) for a weight range of 0.2–62.8 g (Tanabe et al. 1999). Adult tuna also contain high concentrations of DHA (~20–25% in body and viscera oils and ~25–29% in the orbital oil behind the eye socket) and 5–8% EPA. Fish phospholipids typically have a total of 35–40% of these two FA (Polvi and Ackman 1992; Ackman 2000), but generally, phospholipids are <1% of muscle lipid. The balance of the EPA and especially DHA exists therefore in the triacylglycerols of tuna. These high proportions of EPA and DHA are the result of the tuna's natural diet and may therefore be hard to match in fish farming operations. However, the adult frigate mackerel (*Auxis rochei*) fished off Japan shares the same triacylglycerol FA pattern with very high DHA in the orbital oil and a little less in total muscle lipid that ranges from a few percent in dorsal meat to nearly 20% in ventral meat (Morioka et al. 1999). Mackerel species are fairly plentiful in various parts of the world, but fishing *A. rochei* and other species for aquaculture food would likely not be welcomed because there already exists an extensive fishery for direct human use. This leaves aquatic invertebrates as the remaining consideration. Bivalves and shrimp are already farmed on a commercial level, leaving two other groups that can be considered for harvest.

Squid possess a fatty liver or hepatopancreas, the source of an oil in Japan that is sometimes used in aquaculture, as it has essentially the same composition as most fish oils (Table 2). A large part of the world catch is consumed in Japan, but local varieties have been overfished, forcing the fishery onto the high seas for deepwater species. Other squid fisheries (e.g., in Newfoundland), however, have declined because of unknown factors. The Canadian species *Illex illecebrosus* overlaps with *Loligo pealei*, common off the south Atlantic coast of North America. Mantle lipid of both species is between 1 and 2% (Krzynowek et al. 1989) with ~5% EPA and 30–40% DHA, reflecting the tissue's high phospholipid content. Deepwater species tend to have wax esters or diacylglyceryl ethers in their liver lipids (Hayashi 1989), but the extent of these deep-sea resources is unknown. Nearshore European exploitation of squid and octopus for food, however, seems to be sustainable (Sinanoglou and Miniadis-Meimaroglou 1998). Although large-scale culture is unlikely, a recent study has already established the FA needs of five octopus species and suggested that LCPUFA are necessary for larval survival and development (Navarro and Villanueva 2000).

Table 3. Comparisons among phytoplankton FA from three stations (A1, C1, and C5) near South Georgia Island with those of corresponding catches of *E. superba* (Cripps et al. 1999).

	Phytoplankton FA ($\mu g \cdot L^{-1}$)			*E. superba* fatty acids ($mg \cdot kg^{-1}$)		
Component	A1	C1	C5	A1	C1	C5
C14:0	1.3	1.5	1.1	512	24	54
C15:0	0.3	0.3	0.1	14	—	3
C16:0	5	8.3	2.7	765	31	71
C18:0	11.1	22.9	4.9	37	1	3
ΣSAFA	17.7	33	8.8	1328	56	131
C16:1ω7	1.9	2.7	0.5	274	32	70
C18:1ω9	7.2	11.7	2.9	269	22	42
C18:1ω7	0.6	4.1	0.8	126	11	32
C20:1ω9	1.4	2.1	11.7	14	1	0
C22:1ω11	0.3	0.7	0	4	—	0
ΣMUFA	11.4	21.3	15.9	687	66	144
C16:2ω6	0.2	1	0	23	8	15
C18:2ω6	0.9	2.1	1.1	52	6	37
C18:3ω3	0	0.5	1.5	13	2	27
C16:4ω3	0.4	0.5	0	5	11	22
C18:4ω3	0.4	1.7	8.3	23	13	85
C20:4ω6	0	0.4	0	6	1	8
C20:4ω3	0	0	0	6	1	15
C20:5ω3	4.8	11.4	4.7	128[a]	65[b]	260[c]
C22:5ω3	0	0.6	0	—	1	3
C22:6ω3	2.4	3.6	7.1	14	6	39
ΣPUFA	9.1	21.8	22.7	270	114	511
Total	38	76.1	47.3	2282	237	782

Note: Rough volumetric proportions of the main phytoplankton taxa are as follows: A1, one half small diatoms, one quarter pamnesiophytes, and one quarter large diatoms; C1, small diatoms; C5, one tenth dinoflagellates, one quarter chrysophytes, and two thirds small diatoms.

[a]5.6% of FA.
[b]28% of FA.
[c]33% of FA.

"Krill" is a term that was first popularly applied to the Antarctic euphausiid *Euphausia superba*. This organism is ≤6 cm in size and has a lipid system based primarily on glycerol esters (Clarke 1980). Therefore, it does not include wax esters as found in its shelf-dwelling neighbor *Euphausia crystallorophias* (Kattner and Hagen 1998). Other species of krill are smaller in size and the economics do not favor commercial utilization. Table 3 compares three sets of FA data from phytoplankton with those of *E. superba* collected at the same station. Most of the FA, with the exception of C14:0, C16:0, and C18:1 (which are easily biosynthesized), are similar in proportion to those of other marine animals, although euphausiid EPA to DHA ratios are extremely high. As noted by various authors, these LCPUFA are freely available to krill and need not be biosynthesized. Clarke (1980) reported that EPA to DHA ratios were ~2:1 for phosphatidyl

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cholines and ~1:1 for phosphatidyl ethanolamines for *E. superba* from the same location. In the corresponding triacylglycerols, ratios of EPA to DHA were ~3:1. These must, however, be considered as general relationships in the overall FA composition of euphausiids (Table 3). As noted in Table 3, krill from stations A1, C1, and C5 (Cripps et al. 1999) had different diets. If the FA potentially synthesized de novo are C14:0, C16:0, C16:1, and C18:1, then these four (as percentages of the total) are 85% for A1, 50% for C1, and 34% for C5. The figures for EPA are inversely 5.6, 28, and 33% of the total. Samples C1 and C5 are similar in FA composition to those reported by Clarke (1980). In sample A1, an ample supply of phytoplankton carbohydrate prevailed, allowing de novo synthesis of additional C14:0, C16:0, C16:1, and C18:1 into triacylglycerols, thus diluting the EPA and DHA, which could be reserved for functional phospholipids.

In *E. crystallorophias*, wax esters are a complicating factor, but the same FA patterns in triacylglycerols are observed, although C14:0 is relatively less important and C18:1 possibly more important (Kattner and Hagen 1998). In fact, C16:1ω7 and C18:1ω7 should be regarded as one FA with C18:1ω9 as distinctly different. This is because C16:1ω7 is presumably formed from C16:0 by desaturation, so studying C16:0, C16:1ω7, and C18:1ω7 in isolation (Cripps et al. 1999) is rather unlikely to be meaningful. In some samples examined by Clarke (1980), C18:1ω7 exceeded C18:1ω9. In the other reports discussed above, the more common 2:1 ratio for C18:1ω9 and C18:1ω7 seems to have been the rule. This species is described as an omnivore, a further complication in explaining FA compositions.

Commercial interest in exploiting *E. superba* and other similar large euphausiids as sources of protein (11%; Clarke 1980) has waned because of problems of excessively rapid proteolysis (Kolakowski and Gajowiecki 1992). Lipolysis is equally a problem (Sugii and Kinumaki 1982), and even research scientists have to be careful, as Clarke (1980) found that 10–14% of total lipid in carefully preserved krill samples was free FA. This is a well-established phenomenon in fish muscle, although it occurs much more slowly in frozen tissues (Haard 1992). Free FA in amounts exceeding 1% of total lipid in biological or commercial samples should be regarded with suspicion.

Other aquatic sources of essential fatty acids

Pond aquaculture

Despite years of effort, *Spirulena* and *Dunaliella* remain among the few algae successfully harnessed for mass outdoor culture. Both algae require specific growth conditions such as high carbonate, high pH, high light intensity, and (or) high temperature. Such features make these algae well suited to large-scale outdoor aquaculture but only in selected locations. A great deal is now known about the physiology and genetics of these two species, and although these species do not, in known forms, produce appreciable amounts of EPA or DHA (Ben-Amotz et al. 1985), selection of mutants and (or) gene splicing could conceivably be implemented to alter their FA profiles.

Freshwater sources

Historically, most research into FA composition has focused on marine fish/shellfish, reflecting, in part, the economic importance of these fisheries. However, less well studied are marine and freshwater benthic invertebrates and freshwater fish that can contain appreciable quantities of EFA of similar composition to FA found in marine fish (Ackman 1999).

There are undoubtedly many nontraditional freshwater sources of EFA yet to be discovered. We here provide two examples (the amphipods *Gammarus lacustris* and *Hyalella azteca*) of a novel freshwater source for EPA and DHA. The FA compositions of both amphipod species were broadly similar (Fig. 4). FA that were present in both species, at levels exceeding 0.5 μg FA·mg dry weight^{-1}, included palmitic acid (C16:0), oleic acid (C18:1ω9), LA, ALA, ARA, EPA, and DHA. ALA, ARA, EPA, and DHA represented 4.5, 6.7, 19.5, and 13.3%, 4.3, 9.8, 19.3, and 13.4%, and 1.6, 5.0, 28.7, and 3.4% of total FA analyzed in *G. lacustris* from pond 1 and Gursky's pond and *H. azteca* from Redberry Lake, respectively.

There are literally millions of wetlands in the North American central plains. Although less abundant than shallow, more ephemeral ponds, deeper wetlands (>1.0 m) are still very common. These range in surface area from small dugouts to large ponds and may also include extensive wetland complexes. Measured amphipod densities in these wetlands range from <100·m^{-2} (Lindeman and Clark 1999) to several thousands per square metre (Wen 1992) to a high of 57 245·m^{-2} (Hammer et al. 1990), but only in ponds that are deep enough to sustain populations over winter. For example, *G. lacustris* and *H. azteca* require a minimum fall water depth of ~1.5 and ~1.0 m, respectively (D. Lindeman, Canadian Wildlife Service, Saskatoon, SK S7N 0X4, Canada, personal communication).

In a previous study, Arts et al. (1995) obtained estimates of dry weight for adult *G. lacustris* (12.22 mg ± 0.42 SE, n = 96) and *H. azteca* (2.02 mg ± 0.03 SE, n = 416). We used these above data along with FA content measured here (Fig. 4) to produce hypothetical models of potential yields of EPA and DHA in prairie ponds of varying surface area. Mean EPA and DHA concentrations were 2.6 and 1.8 g·kg dry weight^{-1} (*H. azteca*) and 3.3 and 0.4 g·kg dry weight^{-1} (*G. lacustris*), respectively. Our extrapolations suggest that several tonnes of EPA and DHA could be present in a large pond (e.g., 100 × 100 m) where amphipods occur at high densities (Figs. 5 and 6). Further, we would expect concentrations of EPA and DHA within amphipod tissues to be highest in spring and fall, when food quality (in terms of EFA) of freshly sedimenting matter is highest because of the inclusion of diatoms, dinoflagellates, and cryptomonad algae. Amphipods, therefore, represent naturally occurring freshwater sources of EPA and DHA. Such resources may have commercial value, and this could be of particular importance in regions where agricultural diversification is desirable. We report here on naturally occurring levels of EPA and DHA. However, amphipods are readily amenable to aquaculture applications, and the high-productivity, high-light environments on the prairies would be "fertile ground" for such commercial endeavors. Indirect use of

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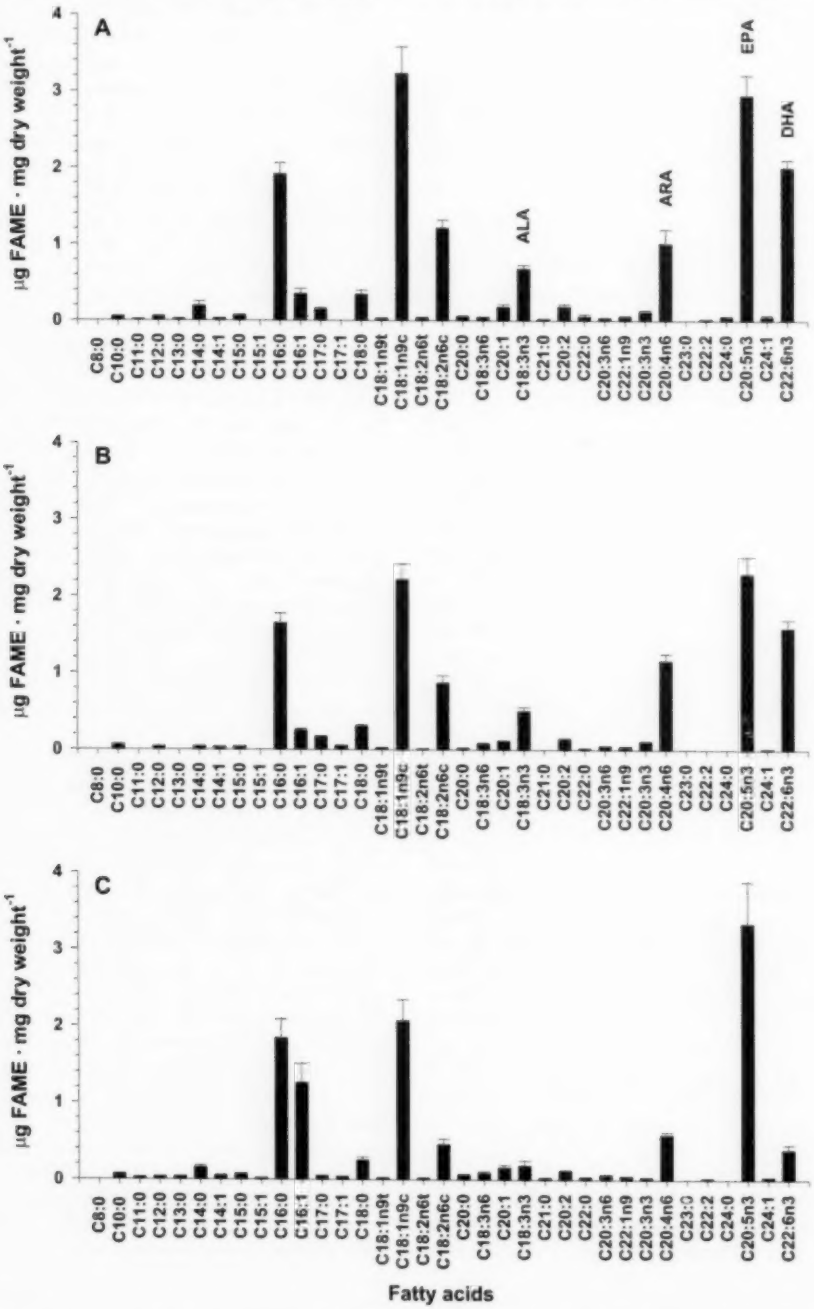
Fig. 4. Fatty acid methyl ester (FAME) concentration in two amphipod species from three wetlands: *G. lacustris* from (A) pond 1 (52°13′N, 106°06′W) and (B) Gursky's Pond (52°09′N, 106°07′W) located in or near the St. Denis National Wildlife Refuge, Saskatchewan, and *H. azteca* from (C) Redberry Lake, Saskatchewan (52°43′N, 107°09′W). Error bars are standard errors.



gammarids and other zooplankton in pond-rearing of rainbow trout destined for human consumption looked appealing three decades ago (Johnson et al. 1970), but flavor problems in the rainbow trout ultimately put a stop to that form of commercialization. However, modern cost-effective refining methods, as well as different commercial interests (e.g., harvesting EPA and DHA), could instill new life into such endeavors. Furthermore, the high protein content "amphipod meal" by-product thus produced would be of potential use in other industries (e.g., livestock feed, petfood).

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Fig. 5. Potential harvest of EPA and DHA in the amphipod *G. lacustris* in wetlands of varying surface area. A depth of at least 1.5 m is assumed.

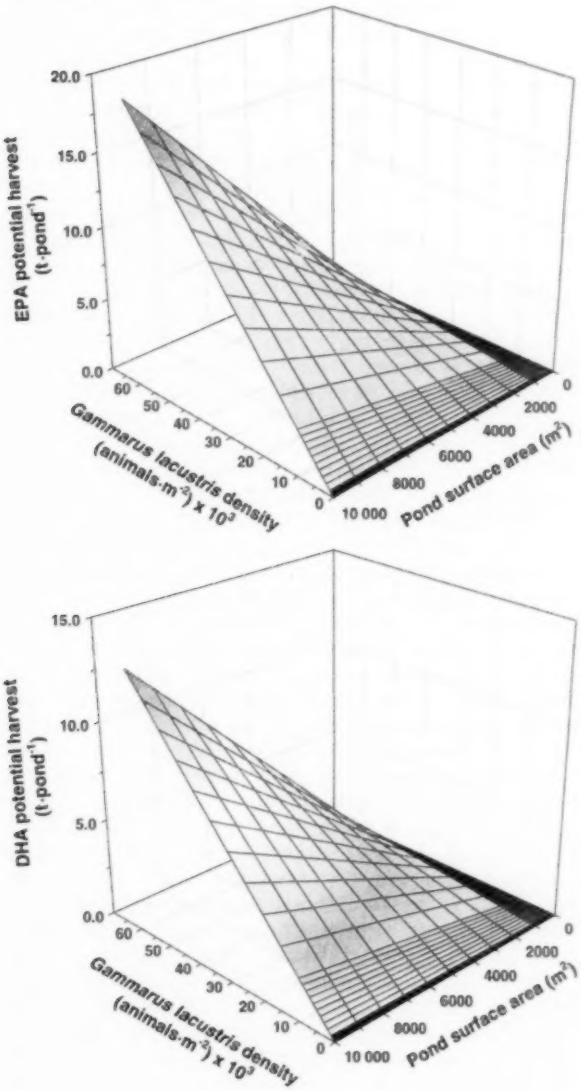
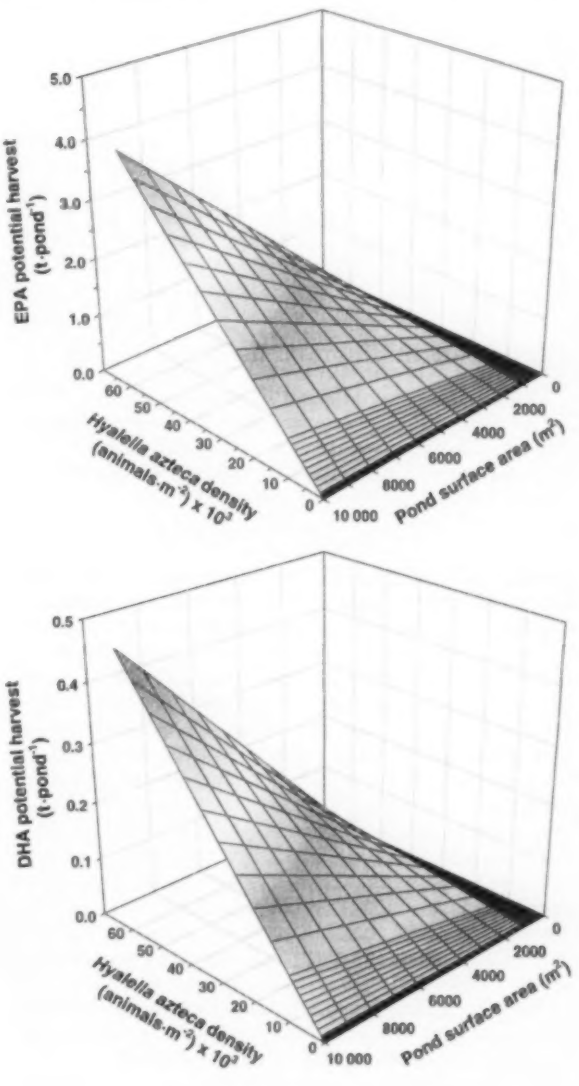


Fig. 6. Potential harvest of EPA and DHA in the amphipod *H. azteca* in wetlands of varying surface area. A depth of at least 1 m is assumed.



Nonaquatic sources

Flax (linseed) and other vegetable oils

Flax oil is currently a popular source of ALA, the precursor to EPA and, ultimately, DHA (but see the section above on terminology for conversion rate estimates). Vegetable oils are normally rich in LA, but a few may also contain γ-linolenic acid (GLA, C18:3ω6). Oils that contain GLA include black currant seed oil, borage oil, and primrose oil. While GLA is the metabolic precursor to ARA, the process of conversion is very slow, requiring participation of the enzyme Δ5-desaturase. This enzyme and the complementary Δ6-desaturase are present in humans at very low levels (Bourre et al. 1990), hindering endogenous biosynthesis of ARA, EPA, and DHA.

Egg yolk lipids

ARA, EPA, DPA, and DHA can be obtained from egg yolk lipids, especially when chickens are flax fed. For example, BurnBrae Farms Ltd. (Lyn, Ont.), which markets Omega-3 chicken eggs (flax-fed chickens), lists the ALA, ARA, EPA, DPA, and DHA content of their eggs as ~331, 45, 6, 10, and 70 mg, respectively, per average 50-g egg. Egg yolks of chickens fed a special diet containing fish meal have especially high EPA+DHA levels (Farrell 1998).

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Heterotrophic fermentation

Using conventional stirred-tank fermenters, economically viable quantities of certain microorganisms that are rich in oils containing desirable EFA such as DHA or ARA can be produced (Becker and Kyle 1998). Martek Biosciences Corp. (Columbia, Md.), for example, has successfully used such mass culture techniques to produce oils rich in DHA (with the marine dinoflagellate *Crypthecodinium cohnii*) and ARA (with fungi such as *Pythium insidiosum* or *Mortierella alpina*). The chief advantages of such techniques lie in consistency and purity of the final FA product. Further, unlike the scenario with fish oils, economies-of-scale have reduced the price of oils derived from organisms raised in fermenters by 10- to 30-fold (D. Kyle, Martek Biosciences Corp., Columbia, MD 21045, U.S.A., personal communication).

Fatty acids and human health

In humans, one of the bases for the heightened interest in EFA includes epidemiological/population studies suggesting that increased fish consumption as a source of ω3 PUFA is often associated with decreased mortality (as well as morbidity) from cardiovascular disease (CVD) (Holub 1988; Leaf 1990). For example, several years ago, it was recognized that Greenland Inuit, when compared with Danes (Bang and Dyerberg 1980), had a significantly lower death rate from acute myocardial infarction despite a high-fat diet (marine based) and only moderate differences in blood cholesterol levels. Furthermore, the higher fish (including EPA+DHA) intakes of the Japanese population relative to North America have been associated with considerably lower rates of acute myocardial infarctions, other ischemic heart disease, and atherosclerosis despite only moderately lower blood cholesterol levels in the Japanese population (Menotti et al. 1999).

The mean current daily intake of EPA+DHA in a typical North American diet is ~0.13 g·day^{-1}, which is severalfold lower than Japanese intakes and only a small fraction of that consumed by the Inuit. Depending on the species eaten, fish consumed two and a half to three times per week would provide an equivalent intake of ~500–600 mg EPA+DHA·day^{-1} (when normalized). These latter intakes are about 4-fold higher than current North American consumption rates. The population data reported by Dolecek (1992) indicated that progressively higher intakes of fish-derived ω3 FA (up to ~650–700 mg·day^{-1}) were associated with a progressive reduction in coronary heart disease related mortality as well as total mortality with no associated increase in total cancer related mortality.

Dietary supplementation and controlled intervention trials with encapsulated ω3 fish oil concentrates can reduce both the progression of CVD and cardiovascular-related mortality including sudden cardiac death in humans, but these have been mostly short-term studies. Various long-term studies (e.g., Daviglus et al. 1997) have also indicated that consumption of fish (two or three servings per week) is associated with lower primary heart attack rates and death from CVD. Fatty acid analyses of serum phospholipid, a biomarker for EPA+DHA intake and status, indicated that DHA levels were inversely correlated with coronary heart disease in men (Simon et al. 1995). Furthermore, intervention studies using fish oil concentrates providing EPA+DHA (combined ω3 FA) at intakes of 2–4 g·day^{-1} over several weeks have shown the ability of these FA to favorably attenuate various risk factors for CVD (independent of any blood cholesterol lowering effect). For example, ω3 FA accumulate to a considerable extent within circulating blood platelets, which is associated with decreased platelet adhesiveness and aggregation and an overall reduction in thrombogenicity (Harris 1997).

Human studies have also revealed the potent ability of EPA+DHA to significantly reduce circulating levels of blood triglyceride (Harris 1997). Moderate elevations in triglyceride (above 100 mg % or 1.1 mmol·L^{-1}) have been associated with a progressively increased risk of coronary heart disease in both men and women (Criqui et al. 1993). Within 2–3 weeks of supplementation, EPA+DHA significantly reduced blood triglyceride levels by ~6–8% per gram EPA+DHA consumed (Harris 1997). In addition, the antiarrhythmic potential of EPA plus DHA (upon accumulation in cardiac tissue) has been considered as yet another important mechanism by which consumption of these FA can reduce cardiovascular-related mortality, particularly sudden cardiac death (Gruppo Italiano per lo Studio della Sopravvivenza nell'Infarto miocardico 1999).

Recent studies have focused on the potential for fish oil supplements (EPA+DHA enriched) to modify clinical endpoints in patients with respect to coronary atherosclerosis and myocardial infarctions. Recently, von Schacky et al. (1999) studied the effect of dietary ω3 FA on coronary atherosclerosis in cardiovascular patients using a randomized, double-blind, placebo-controlled trial. This study revealed that patients with coronary artery disease given ω3 therapy (at levels of ~1–1.5 g·day^{-1}) over 2 years had less progression and more regression of coronary artery disease on coronary angiography (discernible, modest mitigation of atherosclerosis) than did patients on placebo. Fewer clinical cardiovascular events were noted in the ω3 groups. The ω3 supplementation was considered safe and well tolerated. Very recently, the GISSI-Prevenzione trial was reported by Marchioli and colleagues (Gruppo Italiano per lo Studio della Sopravvivenza nell'Infarto miocardio 1999). In this study, 11 324 patients, who had experienced a myocardial infarction, were assigned to supplemental interventions following introduction of a Mediterranean-type diet (which included moderate fish consumption) as well as aggressive treatment with various pharmaceutical agents for cardiovascular care. Approximately half of the patients received an ω3 fish oil supplementation (providing ~0.9 g EPA+DHA·day^{-1}). Over the subsequent interval (up to 3.5 years), the ω3-supplemented subjects were found to exhibit a significant reduction in overall cardiovascular deaths and an approximate 45% reduction in sudden cardiac death. These results support the concept that, independent of blood cholesterol lowering, EPA+DHA intakes (including supplementation) can favorably influence cardiovascular-related mortality (particularly sudden cardiac death) via various mechanisms (a combination of antiarrhythmic, antithrombogenic, lipid-lowering, etc.).

DHA is found at very high levels in the *sn*–2 position of membrane phospholipids in the brain and retina as well as in other tissues and cells (e.g., sperm cells, heart tissue). DHA

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is required at optimal levels in the brain and retina to provide for maximal brain functioning and visual acuity, respectively (Cunnane et al. 2000), especially in infants. Consequently, some expert groups have recommended that DHA should represent at least 0.4% of the total FA in breast milk and infant formula. In order to maintain a minimal level of DHA in breast milk (at 0.4% or more), ~300 mg of DHA needs to be consumed daily. This contrasts with the current mean intake in pregnant and lactating women of only ~80 mg·day^{-1} (Conquer and Holub 1997). The level of DHA in breast milk has been found to be positively correlated (as expected) with dietary fish intake.

Both EPA and DHA, in their fatty acyl-CoA forms, are also esterified to cellular lipid (both phospholipid and nonpolar lipid) and undergo betaoxidation and other metabolic transformations including oxygenation reactions to eicosanoids (prostaglandins, thromboxanes, leukotrienes, etc.). The eicosanoids mediate the potentially beneficial effects of ω3 FA, in part, by replacing ω6 PUFA in cells and tissues, thereby reducing the overall ω6 PUFA to ω3 PUFA ratio and reducing the formation of ARA-derived eicosanoids (Thomas and Holub 1994). The eicosanoids may also affect certain cardiovascular disorders (e.g., thrombogenicity) and proinflammatory conditions (e.g., rheumatoid arthritis; Thomas and Holub 1994).

A number of neurological conditions have also been associated with reduced levels of circulating DHA levels (such as some depressive illnesses, manias, etc.). In many cases, however, controlled studies have not been performed to evaluate whether enhancing DHA intakes and corresponding levels in the circulation and target tissues/cells can improve clinically measured neurological performance. Recently, Stoll et al. (1999) have shown that supplementary ω3 fish oil (containing EPA+DHA) can significantly improve the clinical management of patients with bipolar disorder. A number of studies are now ongoing that utilize DHA alone, EPA alone, or combinations of EPA+DHA with respect to various neurological conditions (depressive illnesses and anxiety disorders, schizophrenia, attention deficit disorder, etc.).

Fish oil concentrates containing EPA+DHA, when given in supplementary form at levels of 3–5 g ω3 PUFA daily over a few months, have also been found to provide significant benefit in patients with various conditions including rheumatoid arthritis and inflammatory bowel disease, including Crohn's Disease (Connor 2000). The mechanisms for these latter effects appear to involve altered eicosanoid synthesis (suppression of ARA-derived eicosanoids including suppressed formations of neutrophil-derived leukotriene B_4, a proinflammatory eicosanoid).

The above findings have led to a dramatic upsurge in intensity by the food industry towards development of nutraceutical and functional food products containing enhanced EFA levels. The goal is to provide products that will improve health in general and positively modify risk factors for chronic disorders (specifically cardiovascular) while simultaneously lowering overall health care costs. Furthermore, the traditional pharmaceutical industry is showing great interest in acquiring ω3 therapeutics for distribution on both a prescription- and a nonprescription-based release. In view of declining fish stocks and the interest among vegetarians to have animal-free sources of these long-chain ω3 FA, there is much recent interest in the development of commercially viable algal (plus other) sources of these FA for use as nutritional supplements and as ingredients for nutraceuticals/functional foods. In addition, these FA can be incorporated into processed food products and into diets/feeds of domestic animals for production of ω3-enriched products including eggs, dairy, and numerous meat products.

In the future, nutraceutical-type products plus numerous food products will be widely available with considerable quantities of EPA+DHA in oil form or as microencapsulated ingredients. These products will offer an overall rise in daily consumption of EPA+DHA, which is currently consumed only in moderate quantities in the form of fish/fish oils. It remains to be established whether the anticipated worldwide increase in EPA+DHA intakes will (*i*) result in significant benefits in reducing morbidity and mortality from CVD, (*ii*) attenuate inflammatory, neurological, and other disorders, and (*iii*) improve the overall quality of life in normal/healthy individuals. Based on published epidemiological, case-controlled, and intervention trials to date, the prospect of overall health improvement and better protection/management of chronic disorders is a reasonable expectation.

Fatty acids and human evolution

Students of the evolution of humans tend to focus on skulls and bones. With respect to the skulls, there are frequent comparisons made on the possible intelligence level of our remote ancestors based on likely cranial capacity. The possibility that the FA in the brain housed in that space might be factors in intelligence has received some attention (e.g., Crawford and Marsh 1989).The relationship between specific LCPUFA and brain intelligence now focuses on those of the ω family simply because DHA and ARA are known to be major FA in the brain lipids of primates. For example, ~60% (dry weight) of the human brain is made of lipids. PUFA make up ~20% (dry weight) of the brain, with ARA and DHA together representing roughly 75% of this mass (Crawford and Marsh 1989; Jamieson et al. 1999). These two FA are at the apices of a parallel system operated by a few enzymes for elongating and desaturating ALA and LA (Fig. 7).

Animal foods were probably important in hunter–gatherer diets, including fish and shellfish sources of long-chain ω3 FA (e.g., Boyd Eaton et al. 1998). Despite this probable long-term adaption over millions of years (Cordain et al. 2000), opposing views favoring plants are not uncommon (Milton 2000). Table 4 shows the probable excess of ALA over LA in the Late Paleolithic diet of largely vegetable origin. The switch to LA > ALA in our contemporary diet is of agribusiness origin and is of concern because of rapidly shifting dietary habits, even in advanced countries such as Japan (e.g., Sugano and Hirahara 2000), where marine foods have traditionally been important.

Unfortunately, aquatic organisms in the food supply have been rather neglected in evolution and diet considerations (Riley 1999). There are reasons for this. Sometimes the excuse is given that fish would be hard for primitive people to catch. Another is that fish bones are fragile and seldom recognized in archaeology. Although Riley's (1999) publication assesses the importance of the introduction of bronze fish-

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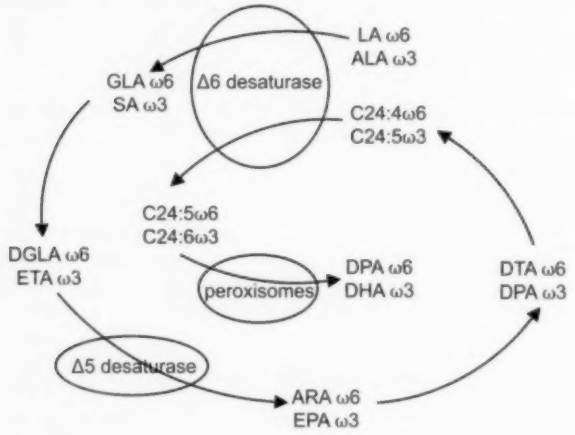
Fig. 7. Metabolism of FA. LA, linoleic acid (C18:2ω6); ALA, α-linolenic acid (C18:3ω3); GLA, γ-linolenic acid (C18:3ω6); SA, stearidonic acid (C18:4ω3); DGLA, dihomo-γ-linolenic acid (C20:3ω6); ETA, eicosatetraenoic acid (C20:4ω3); ARA, arachidonic acid (C20:4ω6); EPA, eicosapentaenoic acid (C20:5ω3); DTA, docosatetraenoic acid (C22:4ω6); DPAω3, docosapentaenoic acid ω3 (C22:5ω3); DPAω6, docosapentaenoic acid ω6 (C22:5ω6); DHA, docosahexaenoic acid (C22:6ω3). Adapted from Yonekubo (1999).



hooks into Crete on diet and social development, that is a technological advance and the era in question is much too recent to show any impact of diet on our basic body FA biochemistry. One must go much further back, probably beyond 4 million years, to contemplate the diet and FA biochemistry of the evermore primitive hominids still being discovered by paleontologists. Unfortunately, our contemporary western fishing habits do not provide much useful reference material, although enormous shell middens in various parts of the world show that quite primitive people had a dietary base of such easily harvested foods. These are unlikely to be from the activities of hunter–gatherers but are evidence of more stable settlements, probably in the most recent stage (10 000 – 100 000 years?) of the evolution of *Homo sapiens*. Nevertheless, the middens suggest that one must look at specific types of FA in aquatic organisms (including invertebrates) for their availability for adaption by early hominids to become the specific types of long-chain FA that are the basis of our contemporary lipid body biochemistry. It should be remembered that "Lucy" (i.e., *Australopethicus*) and her progenitors lived on the edges of freshwater lakes in the African Rift Valley. Our problem is that inadequate attention has been paid to the freshwater milieu as sources of PUFA. Fish containing EPA and ARA (e.g., Kuusipalo and Käkelä 2000) were certainly present, but widely available freshwater invertebrates, such as shellfish and (or) the ubiquitous Amphipoda, likely contributed in establishing our basic FA biochemistry.

It is becoming increasingly clear that, beyond the proximate human health effects of EFA, there are important implications for learning, creativity, and evolution. For example, Horrobin (1998) argued that EFA such as DHA and ARA are major determinants of the richness of the brain's microconnections. He speculated that, in addition to effects on creativity and learning, even diseases such as schizophrenia might be linked to brain lipochemistry. Further, the evolution of the vascular system and, in particular, the placenta, which serves to focus energy and nutrients to one or a small number of progeny during the critical time of brain development has been associated with changes in our access to ARA and DHA (Cunnane et al. 1993; Broadhurst et al. 1998; Crawford et al. 1999). These three lead authors go on to conclude that "brain specific nutrition had and still has significant potential to affect hominid brain evolution" (Broadhurst et al. 1998). Given the intrinsic importance of these crucial biomolecules to our health (and to our environment), we clearly must not underestimate the convergent threats posed by our burgeoning population and the diminishing availability of the more traditional sources of EFA.

Table 4. Late Paleolithic sources of PUFA ($g \cdot day^{-1}$).

PUFA	Plant foods	Animal foods	Total intake
C18:2ω6	4.28	4.56	8.84
C18:3ω3	11.4	1.21	12.61
C20:4ω6	0.06	1.75	1.81
C20:5ω3	0.14	0.25	0.39
C22:4ω6	0	0.12	0.12
C22:5ω3	0	0.42	0.42
C22:6ω3	0	0.27	0.27

Note: Adapted from Boyd Eaton et al. (1998).

Conclusion

If we are to maintain/enhance our present-day health we must take a proactive approach to ensure our sustained access to EFA and, in particular, to EPA, DHA, and ARA. This process could involve some or all of the following steps. First, we should manage ecosystems with a view towards protecting organisms in the food chain that have high concentrations of EFA, principally the oil-rich fish. Second, we should strive to obtain better inventories of species with respect to their EFA content. This is important because it will help identify important natural stores of EFA and better inform us as to spatial and temporal "bottlenecks" in biosynthesis, supply, and (or) distribution of EFA. Finally, as traditional sources for EFA are diminished, we may increasingly have to turn to alternative sources of EFA.

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perspective as "the ongoing development in creation as initiated by God at creation and sustained in providence." B.J.H. wishes to thank Rev. Ed de Haan for this help in formulating the definition of "evolution" as inserted here.

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Marine protected areas in Canada—implications for both conservation and fisheries management[1]

Glen S. Jamieson and Colin O. Levings

Abstract: Legislated marine "protected" areas are now widely distributed throughout tropical and temperate waters, but the nature of human activities actually restricted in any area varies. This ambiguity about what "protected" means has resulted in contradictory claims as to both the benefits and costs of marine protected areas. Here, we give our perspective on the current status of marine resource protection in Canada in general and British Columbia in particular. We first describe and discuss the history of Canadian marine protected areas established to date. Many areas are claimed to be protected, with little understanding by either the general public or even most marine resource experts as to what human activities are actually regulated by legislative designations. Second, we present an overview of biological reasons and objectives for marine protected areas, followed by a review of both the conservation and fisheries management effects and implications resulting from effective renewable resource protection. Finally, we propose a unique qualitative scheme for classifying and describing marine protected areas of different types to determine relative measures of protection.

Résumé : Bien qu'il existe dans les eaux tropicales et tempérées de nombreux pays des zones de « protection » marine établies par voie législative, les activités humaines qui y sont réglementées varient considérablement d'une région à une autre. Cette ambiguïté entourant la notion même de « protection » engendre des affirmations contradictoires sur les avantages et les coûts des zones de protection marine. Nous présentons ici notre point de vue sur la situation actuelle de la protection des ressources marines au Canada en général et en Colombie-Britannique en particulier. Nous décrivons d'abord et commentons l'histoire des zones de protection marine établies jusqu'à maintenant au Canada. Plusieurs zones sont dites protégées, sans que la population en général, et même les spécialistes des ressources marines, ne comprennent bien quelles activités sont de fait contrôlées par les dispositions législatives. Nous faisons ensuite une synthèse des principes biologiques et des objectifs qui sous-tendent l'établissement des zones de protection marine, une revue de leurs effets sur la conservation et l'aménagement des pêches, ainsi qu'un résumé des conséquences d'une protection efficace des ressources renouvelables. Nous proposons enfin une méthode qualitative pour la classification et la description des divers types de zones de protection marine dans le but de pouvoir établir des mesures relatives de protection.

[Traduit par la Rédaction]

Introduction

Marine protected areas are the legislative designation for the protection of specific coastal and marine areas from otherwise unrestricted human activities. The International Union for Conservation of Nature and Natural Resources (IUCN) defines them as "any area of intertidal or subtidal terrain, together with its overlying water and associated flora, fauna, historical and cultural features, which have been reserved by law or other effective means to protect part or all of the enclosed environment" (Kelleher and Kenchington 1992). Rationales for marine protected areas can vary widely, ranging from extensive preservation of relatively pristine environments for their own sake to endangered species protection, continued recreational opportunities, fisheries enhancement, etc., and are largely determined by the legislative Acts that can be used to designate them. The recent considerable interest in marine protected areas in the 1990s in Canada (Shackell and Willison 1995; Canada – British Columbia 1998) and worldwide (Agardy 1995; McArdle 1997*b*) has arisen because of increased recognition that the world's marine and aquatic environments and ecosystems are considerably less healthy and are providing fewer ecosystem services (Costanza et al. 1998) than before humans began impacting these systems on a global scale. Impacts include fishing down the food web (Pauly et al. 1998), overfishing, sometimes to local species extirpation (Jamieson 1993; Powles et al. 2000), pollution (Waldichuk 1990), disturbance and habitat destruction (e.g., through ocean dumping, dredging, and land reclamation through dyking (LOICZ 1999), etc. There is general concern by many that ocean health will continue to decline to increasingly unacceptable levels unless human activities, or their effects, are limited or mitigated in some manner.

Studies of the consequences of marine area protection have been mostly associated with, or at least identified with, tropical waters. They have typically been associated with

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Table 1. Provincial (P) and federal (F) marine protected areas established in Canada by DFO regions over time.

	Pacific		Arctic		Laurentian		Maritimes		Newfoundland		
Decade	P	F	P	F	P	F	P	F	P	F	Total
1910–1919	2	0	0	0	0	2	0	3	0	0	7
1920–1929	0	1	0	0	0	8	0	0	0	0	9
1930–1939	0	2	0	1	0	1	0	3	0	0	7
1940–1949	0	0	0	2	0	0	0	0	0	0	2
1950–1959	4	0	0	4	0	0	0	0	0	1	9
1960–1969	14	2	0	8	0	0	0	0	5	0	29
1970–1979	19	2	0	2	0	1	0	5	0	0	29
1980–1989	21	1	3	3	1	5	0	5	0	0	39
1990–1999	56	1	0	4	0	2	1	0	1	3	68
Total	116	9	3	24	1	18	1	16	6	4	198

Note: Pacific data from Jamieson and Lessard (2000); remaining data from T. Kurvits (DFO, Ottawa, Ont., personal communication).

preservation of long-lived species and particularly vulnerable ecosystems, such as coral reefs (e.g., Kriwoken 1996). While many marine protected areas have been designated in temperate waters (e.g., 124 in British Columbia (B.C.) alone; Jamieson and Lessard 2000), these have often been relatively small (in B.C., 66 (52%) are <1 km^2 in area) and mostly associated with human recreation values rather than ecosystem or species conservation values per se. Recent significant declines in fished species, such as abalone (*Haliotis kamtschatkana*) (Jamieson 1999) in B.C. and northern cod (*Gadus morhua*) (Myers et al. 1997) in Atlantic Canada, have facilitated both the need for a precautionary fisheries management approach (Agardy 1994) and the implementation of marine protected areas as an important fisheries management tool in Canada. These were important considerations in the development and design of the Canadian Oceans Act, passed in January 1997. This Act gave authority to the Minister of Fisheries and Oceans Canada (DFO) to designate specific marine areas, termed Marine Protected Areas (capitalised (MPAs), since this is the specific name designated for marine protected areas under this Act; other federal legislation can establish different marine protected areas, such as national parks (Parks Act), national wildlife areas (Canada Wildlife Act), etc.), for special protection, with specific human activity exclusions defined on a site-by-site basis. Other Canadian provincial government departments and ministries with the appropriate mandate have also established marine protected areas, and these have been termed marine parks, sanctuaries, reserves, wilderness areas, wildlife areas, ecological reserves, "protected areas," and so on.

The purpose of this paper is to give our perspective on the current status of marine resource protection in Canada in general and B.C. in particular and to propose a qualitative scheme for the classification and description of different marine protected areas. We first describe and discuss the history of Canadian marine protected areas established to date and their types. Many areas are claimed to be protected, with little understanding by either the general public or even most marine resource experts as to what human activities are actually regulated by legislation. There are, for example, 10 different types of legislated marine protected areas (including Parks Canada's national marine conservation areas (NMCAs), which are expected to soon be established) in B.C. alone, each with its own characteristics. Second, we present an overview of realistic biological reasons and objectives for marine protected areas, followed by a review of the results of conservation. We specifically discuss the implications of restricting human activities on themes for conservation such as community dynamics, intraspecies genetic and (or) behavioural diversity, and habitat, sensitive species, and biodiversity conservation. Third, we discuss the implications of marine protected areas for fisheries management, specifically topics such as reference, or "control," sites, experimental management, the optimal proportion of the coast in reserves, and marine protected area networks. Finally, we propose a new qualitative scheme for classifying and describing marine protected areas of different types so that a relative measure of level of protection (i.e., restrictions on human activities) can be determined by the type of designation.

History of marine ecosystem protection in Canada

In this section, we discuss the historical pattern for establishment of marine protected areas in Canada, the relative geographical areas protected by region, and what the term "protected" actually means in terms of both habitat and species protection. We also summarise what federal and provincial Acts are available to establish protected areas, how governments have used them to define protected areas, and associated enforcement challenges.

Areas, primarily terrestrial, have been protected in Canada since at least 1885 when the first national park was established in Banff, Alberta. However, as will be discussed below, calling an area protected in Canada may not actually restrict many human activities. Protected areas established by provinces have been set aside to protect a province's diverse natural, cultural heritage, and recreational values (e.g., British Columbia 1993). In B.C., protected areas are defined as inalienable: the land and resources may not be sold, and they are areas where no industrial extraction of nonrenewable resources or development is permitted. The first provincial protected area in B.C. with a marine component, and the first provincial terrestrial park established there, was Strathcona Provincial Park. This park was established in B.C. in 1911. There are currently many other primarily terrestrial parks that also have a relatively minor marine portion (Jamieson and Lessard 2000). The first marine protected area established in B.C. based only on marine aesthetic values was Maquinna Marine Park, established in 1955. Most marine

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Table 2. Legislated areas with a marine component by general type (provincial designations may not all be exactly similar) by DFO region.

	Pacific[a]	Central and Arctic[b]	Laurentian[b]	Maritimes[b]	Newfoundland[b]	Total
Provincial total	**116**	**3**	**1**	**1**	**6**	**127**
Ecological reserves	15	0	0	0	6[c]	21
Provincial parks	81	3[d]	1	1	0	86
Wildlife management areas	4	0	0	0	0	4
Wildlife reserves	15	0	0	0	0	15
"Protected areas"	1	0	0	0	0	1
Federal total	**9**	**24**	**18**	**16**	**4**	**71**
National park (reserves)	1	5	0	2	1	9
National marine parks (= national marine conservation areas)	0	0	1	0	0	1
Migratory bird sanctuaries	5	17	15	7	3	48
National wildlife areas	2	2	2	7	0	13
Marine protected areas	1(3)[e]	0	0	(1[e])	0	1[e]
Grand total	**125**	**27**	**22**	**17**	**10**	**198**

Note: Great Lakes protected areas are not included here, as they are freshwater.
[a]Jamieson and Lessard (2000).
[b]DFO (1999) and T. Kurvits (DFO, Ottawa, Ont., personal communication).
[c]Anderson et al. (2000).
[d]Ontario = 2, Yukon = 1.
[e]Candidate MPAs; the first MPA in Canada was gazetted on October 28, 2000.

protected areas have been established in B.C. in the last few decades (Table 1).

In eastern Canada, the first provincial marine protected areas to be established were four wildlife reserves (now called ecological reserves: Cape St. Mary's, Witless Bay, Hare Bay, and the Funk Islands) in Newfoundland (Table 1) by the Provincial Department of Tourism, Culture and Recreation in 1964 (Table 2) to protect seabirds (Anderson et al. 2000). There has only been one marine protected area based only on marine aesthetic values established in eastern Canada to date, the Saguenay – St. Lawrence Marine Park, established in 1998 as a joint initiative of the federal Department of Canadian Heritage and the Province of Quebec.

The first marine protected areas established solely by the federal government were migratory bird sanctuaries (MBSs) established through the Canadian Wildlife Service, Environment Canada. The first in B.C., Victoria Harbour, was established in 1923, and the first in Atlantic Canada, Port Joli Basin in Nova Scotia, was established in 1915. The role of an MBS is to protect migratory birds — shorebirds, waterfowl, and seabirds — from hunting and other sources of disturbance at their breeding grounds and on migratory stopovers. Environment Canada has another marine protected area designation, national wildlife areas, that focuses more on protecting bird habitat (see Jamieson and Lessard 2000).

Relative to the rest of Canada (Atlas of Canada: total Canadian coastline is 243 792 km; the total provincial coastline, i.e., excluding the Yukon, Nunavut, and Northwest Territories, is 81 689 km; values include mainland coast and perimeters of both major and minor islands), B.C. has a relatively small coastline (25 725 km, 11 %), yet it has 63% of the 198 legislated marine protected areas in all of Canada (Table 2). B.C. has a total marine protected area of 2252 km^2 (55 and 22% of this area in provincial parks and ecological reserves, respectively). An additional 3458 km^2 is in the proposed Gwaii Haanas National Marine Park Reserve, which while its boundaries are established has officially yet to be gazetted (Jamieson and Lessard 2000). DFO divides the coast in the rest of Canada into four management regions (DFO 1999). The total marine area currently protected by statutes other than the Oceans Act in each of these regions is as follows: Laurentian (southern Quebec), 1514 km^2 (98% federal, with 75% of this area in national parks); Maritimes, 80 km^2 (99% federal, with 54% national parks, 26% MBSs, and 20% national wildlife areas); Newfoundland (including Labrador), 1084 km^2 (47% national parks and 52% provincial ecological reserves); Arctic, 21 152 km^2 (98% federal, with 63% MBSs, 30% parks, and 7% national wildlife areas) (T. Kurvits, DFO, Ottawa, Ont., personal communication).

Parks Canada approved a National Marine Parks Policy in 1986, with a revised NMCA Policy in 1994. An agreement to establish the first NMCA — Fathom Five in Georgian Bay in Lake Huron (note: the above Parks Canada policy statements do not differentiate between the Great Lakes and oceans) — occurred in 1987. In 1988, the signing of a federal–provincial agreement committed the governments of Canada and B.C. to work towards the creation of the Gwaii Haanas NMCA in the Queen Charlotte Islands. Parks Canada has divided Canada's three oceanic coasts and the Great Lakes system into 29 marine regions, each with a distinct combination of geological features, coastal landforms, oceanographic processes, and marine-associated wildlife (http://parkscanada.pch.gc.ca/nmca/nmca/index.html). Its long-term goal is to represent each region within a system of NMCAs.

The federal department with a strong marine resource management mandate, DFO, has only had the authority to establish marine protected areas since January 1997, when the Oceans Act was approved. This Act gave authority to the Minister of DFO to designate MPAs for special protection for one or more of the following reasons: (*i*) the conservation and protection of commercial and noncommercial fishery resources, including marine mammals and their habitats, (*ii*) the conservation and protection of endangered or threatened marine species and their habitats, (*iii*) the conservation

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and protection of unique habitats, (*iv*) the conservation and protection of marine areas of high biodiversity or biological productivity, and (*v*) the conservation and protection of any other marine resource or habitat as is necessary to fulfill the mandate of the Minister.

In contrast with the proposed Marine Conservation Areas Act, the Oceans Act does not apply to the Great Lakes. As of September 2000, five candidate MPAs had been established in the Pacific (four) and Atlantic (one). Numerous additional Areas of Interest are also being proposed through various planning processes. The other conservation tool available to fisheries resource managers is fisheries closure under the Fisheries Act. However, since such closures are by regulation rather than legislation, like Ramsar sites (Anonymous 1971) and biosphere reserves (UNESCO 2000), they are not considered MPAs (see "Types of marine protected areas" section).

What does "protected" mean?

There are two general categories for marine protected areas: those that were primarily established to preserve habitats and ecosystems (parks, etc.) and those that are focused on the protection of individual species or species groups such as shorebirds, waterfowl, and seabirds (MBSs, etc.). In the latter case, restrictions on human activity typically only apply when the protected species are present (often only in the spring or fall with migratory birds) and may provide little protection of habitat per se. Forty-eight of the 71 existing federal marine protected areas nationwide are of this latter type (Table 2).

The remaining 150 marine protected areas nationwide — 127 are provincially legislated, with 116 in B.C. — primarily protect habitat identified on a biophysical basis but not necessarily the water column, which is also fish habitat (Table 2). Fishing occurs in most existing designated marine protected areas in Canadian coastal waters, often over the objections of the province that established the marine protected areas (e.g., B.C. (K. Morrison, Ministry of Environment, Lands and Parks, Victoria, B.C., personal communication). This occurs because the federal government of Canada is the senior level of government and has the mandate to manage renewable marine resources, and so its fisheries regulations supersede provincial regulations. The consequence is that at present, fishing can and does occur in virtually all areas that might be desired to be fully protected by the provinces.

The level of habitat protection provided to any marine protected area is somewhat determined by the legislative Act that was used to establish it but sometimes is primarily determined on a site-by-site basis, typically in consultation with local communities and interest groups. Restrictions on human activities can be grouped into three basic categories. (*i*) Prevention of habitat destruction or modification (nonrenewable resource extraction (water diversion, mining, etc), ocean dumping, dredging, etc.). The habitat provisions of the federal Fisheries Act provide penalties under the criminal code for the unauthorised alteration or disruption of fish habitat and the deposition of deleterious substances. However, to our knowledge, this Act has never been used in the context of prosecution for habitat changes in a protected area. Environment Canada regulates ocean dumping under the Canadian Environmental Assessment Act. (*ii*) Prevention of species harvest or exploitation (i.e., logging, fishing, or hunting, with restrictions often species specific). (*iii*) Prevention of species' disturbance (e.g., feeding wildlife or interfering with their natural behaviour, reproduction, and rearing of young).

From a habitat protection perspective, provisions of the Fisheries Act are reactive rather than proactive. The Oceans Act and the proposed National Marine Conservation Act provide no minimum level of protection for any species or habitat, with protection of habitat and species to be determined on a site-by-site basis. Protected areas established under either Act can be homogenous, i.e., a common level of protection applies over the entire protected area, or the marine protected area can be zoned internally, with different levels of protection applied to each zone. Zoning is particularly useful for separating incompatible activities, protecting resources, and reducing conflict (Bohnsack 1996). For example, a specific MPA might have a core area where no species may be harvested ("no-take" area), harvest of only migratory or pelagic species, such as salmon or herring, over the remaining area, and no ocean dumping, dredging, or nonrenewable resource extraction (mining, etc.) over the entire area. Similarly, a specific NMCA, which tend to be large areas, may have a number of internally zoned no-take areas, with variable levels of harvest of particular species permitted in other specific zones.

The option of having a very large marine protected area, such as the entire Strait of Georgia in B.C., with internally zoned areas thus compares relatively equally to the idea of a network of smaller marine protected areas. The main difference between them is in the method and perhaps ease with which monitoring and adaptive management (Walters 1986) can be effected. Future change in the spatial pattern and relative sizes of areas of higher protection may be easiest to effect within a single protected area. Australia's Great Barrier Reef, the largest existing legislated marine protected area in the world, is an example of the former case. As presently proposed (Canada – British Columbia 1998), a network of MPAs, i.e., many relatively small Areas, is the management approach anticipated to be effected through the Oceans Act (C. Masson, DFO, Nanaimo, B.C., personal communication). NMCAs, although intrinsically like the Great Barrier Reef in concept, will probably be larger than MPAs but not large enough to include whole identified ecoregions (http://parkscanada.pch.gc.ca/nmca/nmca/index.html). In B.C., for example, the proposed Gwaii Haanas NMCA, which will be the largest marine protected area in Pacific Canada at 3457.5 km^2, is considerably smaller than each of the two ecoregions that it straddles (see http://parkscanada.pch.gc.ca/nmca/nmca/pacific/index.htm).

It should also be pointed out that different marine protected areas may overlap each other. Thus, the XwaYeN (Race Rocks) MPA, gazetted on October 28, 2000, will overlap B.C.'s existing Race Rocks Ecological Reserve. Similarly, the potential Gulf Islands NMCA, if established, will overlap many existing provincial marine protected areas (provincial parks, ecological reserves, designated areas, etc.; Jamieson and Lessard 2000) and possibly some future MPAs, such as the candidate MPA at Gabriola Pass.

The issue of federal and provincial ownership of the seabed and overlying water has some relevance, as it can deter-

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mine what Act is used to protect an area and the types of marine protected areas that can thus be established. In Canada, the federal government alone has the mandate to protect and conserve (*i*) migratory bird species, all marine species (except in B.C., where oysters have been delegated to B.C. to manage), and most anadromous species, (*ii*) habitat below high tide that falls under federal legislation, such as recognized fish habitat or habitat in national parks, NMCAs, and national wildlife areas, and (*iii*) habitat in "offshore" areas, i.e., within the Extended Economic Zone (EEZ) seaward of recognised provincial land. The provinces' conservation mandate includes all other species and habitats. There is some disagreement between Canada and B.C., at least as to how the "offshore" is determined. Provincial land in B.C. is all land between "headland to headland," and while this is accepted by the federal government, there is a difference of legal opinion as to what constitutes a "headland." There is agreement that most of the bottom of the Strait of Georgia is provincial land, but B.C., for example, also claims that this definition defines a line from the northern tip of Vancouver Island and the southern tip of the Queen Charlotte Islands. Such a boundary would make Hecate Strait and Queen Charlotte Sound provincial land, but this boundary has not been accepted by the federal government and has not yet been resolved by a court.

In Pacific Canada, most existing marine protected areas (Table 2) are provincial (116, 94%), nearshore, and relatively small (Jamieson and Lessard 2000). In eastern and arctic Canada, most marine protected areas are federal (62, 82%), and most are MBSs (Table 2). MBSs in eastern Canada are relatively small in area (average marine area = 14 km^2, SD = 24 km^2) and focus on migratory staging areas, but those in the Arctic tend to be larger and focus on breeding grounds, with marine portions averaging 841 km^2 (SD = 1 650 km^2) (T. Kurvits, DFO, Ottawa, Ont., personal communication).

Most provincial marine protected areas protect habitats or ecosystems, and only incidentally those marine species that are not of interest for commercial or recreational harvest. Many habitats that are of commercial or recreational fisheries interest are only protected under the Fisheries Act. The DFO Minister can authorise habitat disruption or alteration, but only after specific compensation or mitigation procedures are agreed to. Charges can only be laid after damage has occurred if authorisation to cause damage was not obtained. Most federal marine protected areas are MBSs, and so primarily protect only a few species and little habitat per se. The federal exceptions are with the nine national parks with a marine component, which protect habitat and most marine species but often still permit fisheries for those species that were being exploited at the time a national park was established ("grandfathered" fisheries). Thus, for example, fisheries for Dungeness crab (*Cancer magister*) and Pacific salmon (*Oncorhynchus* spp.) are still permitted in Pacific Rim National Park Reserve in B.C. What this means from an operational perspective is that in the marine environment, there are virtually no areas at this time where all marine species and habitats are simultaneously protected through legislation, i.e., as an marine protected area. In B.C., only five areas are totally protected, all of which are small. Those that have a complete ban on fishing through fisheries regulations and are also protected from habitat alteration are Porteau Cove Marine Provincial Park and XwaYeN (Race Rocks) MPA (42 and 251 ha, respectively, the only legislated marine protected area of the five), a 0.85-ha research study site off Point Atkinson in West Vancouver, and Whytecliffe Municipal Park in West Vancouver (19 ha). The fifth area is the immediate area (<1 km^2) around Williams Head Penitentiary near Esquimalt where a ban on all fishing is enforced by guards to prevent inmate escape. Other areas in B.C., as mapped by Jamieson and Lessard (2000), may have some fishing closures superimposed on marine protected areas, but these are either not for all species or not for the entire area. Fishing closures relative to marine protected areas have also been mapped in Newfoundland and Labrador (Anderson et al. 2000), and there, no areas are fully protected.

In addition, the above does not mean that effective protection is provided through enforcement at marine protected areas all the time (Jamieson 2000). If a species' value is high enough, as it is with abalone, illegal harvest, or poaching, may occur and particular populations may be relatively depleted (Wallace 1999*a*, 1999*b*). The only continuous and totally effective enforcement in Canada appears to be around Williams Head Penitentiary. Legislating protection and actually enforcing it are two quite different issues, with the former easiest to effect.

Types of marine protected areas

Gubbay (1995) and Agardy (1997) provided brief global perspectives of MPAs and summarised the six categories of protected areas now recognised by the IUCN (1994), based on what the protected areas are managed for. However, while some marine protected areas have existed for many years and are described in each respective country through their legislative designations, descriptions of protected areas in the published literature are limited, with the last effort being that of the IUCN (1994). In recent years, however, there have been some documents produced that give these data, particularly in the northeast Pacific. There are now summary documents for California (McArdle 1997*a*), Washington (Murray 1998*a*, 1998*b*), and B.C. (Jamieson and Lessard 2000). Documentation for eastern Canada is less detailed, but marine protected areas have been listed by Nicholls (1998), DFO (1999), and Anderson et al. (2000). In addition, the Gulf of Maine Council has an marine protected area project that is still ongoing, with one of the outputs a database currently under revision of Canada–U.S. protected areas (http://www.gulfofmaine.org/library/mpas/mpa.htm). Some of these documents include designations for areas that are not legislated protected areas, which we consider pseudo marine protected areas because they have no management or regulatory authority associated with them. This includes United Nation's designated biosphere reserves (UNESCO 2000), which are established around locally legislated protected areas; Ramsar sites (Anonymous 1971), which focus on the conservation and wise use of wetlands by national action and international cooperation; national whale sanctuaries, which provide voluntary guidelines for vessel traffic in the presence of specific whale species (DFO 1999); and municipal parks (see Jamieson and Lessard 2000), which are established through local council designation. However, in at least some of the marine protected areas included in the above

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summary documents, agencies with management authority have established closures that complement the boundaries of the above pseudo marine protected areas. Thus, functionally, their establishment may have resulted in the protection of marine areas from some potential human impacts.

To understand the actual level of protection that is actually enforced at any particular legislated marine protected area, it is necessary to know the overlapping regulations that restrict human impacts at each site. This information has been compiled for B.C. by Jamieson and Lessard (2000) and for Newfoundland and Labrador by Anderson et al. (2000). The problem with databases on fishery closures is that protection established through regulation is relatively dynamic, with regulations relatively easily created, modified, or deleted on an annual basis. Databases describing them need to be updated frequently to be accurate, but documents like those referenced above at the least provide a snapshot picture in time to compare future situations against.

The legislative tools, designations, and mandates for marine protected areas that have been established in B.C. are listed in Table 3. There are five provincial types of marine protected areas and potentially five federal types (no NMCAs have currently been designated in Canada; the first MPA in Canada, XwaYeN (Race Rocks) MPA, was recently announced). The federal types of marine protected areas described in Table 3 include all the types of federal marine protected areas that can presently be established anywhere in Canada. In arctic and eastern Canada, two types of marine protected areas (provincial, or territorial, parks and ecological reserves) have been established with regional legislation (Table 2).

With many new marine protected areas being established worldwide each year, it is difficult to maintain an up-to-date inventory of their numbers and characteristics. There is no accurate current collective summary of the types of marine protected areas that occur worldwide that we are aware of, although past summaries exist for some countries (e.g., Australia, McNeill 1994). This may be in part because there is no universally accepted method for categorising areas on the basis of mandate or level of protection provided. Also, the establishment of marine protected areas is currently an area of particular interest in many countries, with legislation allowing the establishment of such areas being developed or only recently just developed. Worldwide, many new marine protected areas are being proposed or considered, and many have been established over the past decade (e.g., see Table 1 for Canada). Increased interest in marine protected areas has resulted for a number of reasons, including (*i*) that the world's exploited fish stocks are now almost fully exploited and yields are declining from many fished populations, (*ii*) increased public awareness of the need for increased marine resource protection, and (*iii*) increased recreational and ecotourism use of the marine environment.

Marine protected area objectives and effects

Biologically, some of the major objectives of marine protected areas are to protect and conserve renewable marine resources (including marine birds and mammals), unique habitats and ecosystems, and (or) representative examples of the marine environment (Canada – British Columbia 1998). Environmental managers are attempting to conserve or reestablish natural resources in important and representative areas, and having the authority to restrict human activities that impact natural resources is essential in this regard. Defensible methods to determine specific sites or networks from the myriad of MPAs are also important (Levings and Jamieson 1999). Resource managers try to establish procedures for sustaining stable exploitation, but because of social and economic pressures and periodic unanticipated natural fluctuations in abundances of targeted species or changes in habitat conditions, they are frequently tasked with the need to rebuild depleted populations. In both instances, marine protected areas are increasingly recognised as an important resource management tool. Having specific areas clearly defined as protected areas where identified actions cannot occur eliminates the pressure for managers to continually restrict developers or exploiters of natural resources. For managers of exploited renewable resources, having refugia where species can reproduce at their maximum rates can provide insurance against possible overexploitation of harvested resources and improved opportunities for resource recoveries. Exploitation of one or more species may be restricted to ensure that reproductive refugia exist for these species. The goal is to provide reproductive refugia that will help better sustain harvesting in adjacent exploited areas.

Where harvesting is not permitted within protected areas, there are three main biological effects that marine protected areas are likely to influence: the demographic characteristics of species' populations, community dynamics and ecological functions within ecosystems, and the maintenance of genetic and (or) behavioural diversity within species. Each of these factors is important, as collectively, these effects maintain ecological integrity. The nature and extent of effects will be determined by the level of protection offered, and in the following, it is assumed that no harvests or habitat disruptions are permitted in at least the no-take portions of marine protected areas. These no-take areas will be generically referred to below as reserves, as used by Ballantine (1991). This is similar to Allison et al.'s (1998) definition of reserves as areas of high, spatially explicit protection.

Demographic characteristics

Marine reserves have been proposed as "reproductive refugia" (e.g., Carr and Reed 1993; Tegner 1993) where adults of spatially persistent, or resident, species would be permitted to increase in abundance and fecundity, the latter because older individuals are often larger. Increased population fecundity could compensate, via the export of larvae, for possible overfishing in areas outside the reserve (Quinn et al. 1993; Hastings and Botsford 1999). It is intuitively logical, and supported by all studies to date, that in the absence of fishing, the number of resident animals approaching the asymptotic size of the species will increase (e.g., Roberts 1995; Russ and Acala 1996). The reproductive characteristics of a population in a reserve will gradually revert to what might have been expected before significant fishing occurred. Given larger population sizes with older and more fecund individuals (Brooks et al. 1997), reproductive output for the protected portion of the population would then tend to be maximised. Factors influencing reproductive contributions from

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Table 3. Federal and B.C. statutory powers for protecting marine areas.

Agency	Legislative tools	Designations	Mandates
Fisheries and Oceans Canada (federal)	Oceans Act	Marine Protected Areas	To protect and conserve: •fisheries resources, including marine mammals and their habitats •endangered or threatened species and their habitats •unique habitats •areas of high biodiversity or biological productivity •areas for scientific and research purposes
	Fisheries Act	Fisheries closures	Conservation mandate to manage and regulate fisheries, conserve and protect fish, protect fish habitat, and prevent pollution of waters frequented by fish
Environment Canada (federal)	Canada Wildlife Act	National wildlife areas	To protect and conserve marine areas that are nationally or internationally significant for all wildlife but focusing on migratory marine birds
	Migratory Birds Convention Act	Migratory bird sanctuaries	To protect coastal and marine habitats that are heavily used by birds for breeding, feeding, migration, and overwintering
Parks Canada (federal)	National Parks Act Proposed National Marine Conservation Areas Act	National parks Proposed marine conservation areas	To protect and conserve for all time marine conservation areas of Canadian significance that are representative of the five natural marine regions identified on the Pacific coast of Canada and to encourage public understanding, appreciation, and enjoyment
Ministry of Environment, Lands and Parks (provincial)	Ecological Reserve Act	Ecological reserves	To protect: •representative examples of B.C.'s marine environment •rare, endangered, or sensitive species or habitats •unique, outstanding, or special features •areas for scientific research and marine awareness
	Park Act	Provincial parks	To protect: •representative examples of marine diversity and recreational and cultural heritage •special natural, cultural heritage, and recreational features To serve a variety of outdoor recreation functions including: •enhancing major tourism travel routes •providing attractions for outdoor holiday destinations
	Wildlife Act	Wildlife management areas	To conserve and manage areas of importance to fish and wildlife and to protect endangered or threatened species and their habitats, whether resident or migratory, of regional, nationa,l or global significance
	Land Act	Designated wildlife reserves	To reserve Crown land for specified periods for a variety of reasons, including the protection of sensitive habitat or habitat important for the conservation or well-being of species
	Environment and Land Use Act	"Protected areas"	To protect: •representative examples of marine diversity and recreational and cultural heritage •special natural, cultural heritage, and recreational features

Note: Modified from Jamieson and Lessard (2000).

refugia are species fecundity, parameters influencing larval survival (e.g., density dependence) and dispersal (i.e., the larval transfer function), and the relative proportion of the species' population that occurs in the reserve area. Modelling (e.g., Man et al. 1995) suggests that increased overall population reproductive output from protected areas

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has the potential to significantly support adjacent fisheries. Conversely, managers may have a false sense of security if inappropriate placing of reserves makes them functionally inadequate (Carr and Reed 1993; Tegner 1993). Inappropriate siting of reserves could involve situations where relevant spawning habitat was not protected or where larvae were exported to unsuitable habitat. Depending on home ranges in a harvested stock and the distances that larvae drift, benefits from reserves may be adjacent to and (or) remote from a reserve.

Another manner in which reserves may be important is through the emigration of exploitable-sized individuals across the border of the reserve into exploited areas (Guénette et al. 1998; Lauck et al. 1998). Opportunity for "spillover" of harvestable sizes is greatly influenced by reserve location, size, and shape. Documentation of spillover is relatively limited (e.g., Attwood and Bennett 1994), both because it is often difficult to determine the origin, i.e., from closed or exploited areas, of untagged harvested individuals and because the strongest evidence would occur with study of relatively heavily exploited, large, old individuals with limited mobility. Few temperate water species meeting these criteria have been studied in this manner, but in Canada, species such as Pacific rockfish (*Sebastes* spp.), lingcod (*Ophiodon elongatus*), Dungeness crab, and American lobster (*Homarus americanus*) seem particularly appropriate for study. Alcala and Russ (1990) showed that with the opening of a reserve to fishing, regional catch-per-unit-effort declined by 57% for hook-and-line, 58% for gillnet, and 33% for trap fishing, even though the fished area was larger afterwards because it then included the previous reserve area. However, this was in a tropical location (the Philippines), and results may have been influenced by site-specific factors because tropical species tend to have smaller home ranges with reduced potential for spillover. Rowley's (1992) literature review concluded that what data do exist support spillovers occurring but that data are limited overall.

The opposite perspective is that reserves would inherently reduce yields in existing fisheries, if for no other reason than that they would reduce the area currently accessible to a fishery. This concern has often tended to impede the establishment of reserves because of initial opposition by fishers. Many theoretical studies (e.g., Sladeck Nowlis and Yoklavich 1998; Hastings and Botsford 1999) have now addressed this point. Typical assumptions are that adults are relatively stationary and will not move outside the protected area, that larval settlement distribution along the coastline is independent of location, and that all density dependence occurs at the time of settling and only depends on the density of settling juveniles. Under these conditions, these theoretical studies concluded that management of fisheries for relatively mobile species using either protected areas or management through effort controls produces similar fishery yields. The greatest potential increases in yield as a result of protected areas are achieved with spatially persistent, i.e., relatively sedentary, species. Some studies have been less conclusive: DeMartini (1993) suggested that catches might be increased or at least maintained for some species, while they would decline for others, Holland and Brazee (1996) suggested that catches might increase, but only if effort was excessive prior to creation of the protected area and if further expansion was controlled after the reserve was created, and Hannesson (1998) suggested that area closures will generally reduce overall catches and increase costs. In summary, results may be species and site specific, and there is a strong need for field studies to test hypotheses.

There has been only one evaluation (Wallace 1999*b*) of the biological consequences of no-take areas in Canada. Increases in average individual size and abundance of abalone were observed, but population fecundities and fishery spillover effects were not investigated per se.

Community dynamics

The direct consequences of harvesting species are a reduction of individuals because of removals and the potential loss of future individuals because of decreased fecundity, reproduction, and growth at the population level. The indirect effects of exploitation include (*i*) the potential loss of food items for other species that may at least partially depend on the exploited species, (*ii*) a removal of predators that may represent a significant population control component for many species, (*iii*) the incidental or intentional, depending on which species are being harvested, destruction of important habitat structuring species (e.g., corals) upon which many species depend, and (*iv*) the modification or destruction of other habitat characteristics such as sediment type. The presence of reserves would prevent any of this from occurring from fishing.

One of the problems of documenting community effects in the present, typically many years after full exploitation of many local species has occurred, is that contemporary community dynamics may not be representative of what existed in the preexploitation period. Important species may have been extirpated from a local environment (Koslow et al. 1988; Roberts and Polunin 1993), and both the resulting community structure and the dominance of species may now be significantly different from those that used to occur. An example from the Pacific is the consequence of sea otter (*Enhydra lutris*) extirpation. Estes (see Estes (1996) for a review) and his students have documented the influence of sea otters on the relative abundances of a wide range of different species through their predation of subtidal benthic invertebrate grazers, such as sea urchins and abalone. In the absence of sea otters, grazers abound, consuming sufficient macroalgae to create what is locally known as sea urchin "barrens." Kelp beds are largely prevented from establishing, and since these beds provide important cover and habitat for many other species, relative abundances of these latter species in the nearshore environment have been substantially modified.

Species do not have to be extirpated to have their structural roles in the community impacted by fishing. When intertidal grazers such as keyhole limpets (*Fissurella* spp.) are the targeted species, as occurs in Chile, their harvest resulted in the luxuriant growth of algae, which reduced the space available for numerous other species in the intertidal and thereby altered the diversity and species assemblages in the community (Moreno et al. 1984; Durán et al. 1987). Algae were only abundant in midintertidal areas where limpets were continuously harvested.

Thus, present fishers and today's general public, who may not have been present when a pristine environment existed,

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often assume that the current species biodiversity, community structure, and relative mix of species observed now are relatively normal. The immense impact that humans have had on many marine communities is often largely unrecognised until studies document the effects, as in Chile (e.g., Castilla and Bustamente 1989) and Australia (e.g., Underwood 1993). On the west coast of Canada, there is substantial documentation about how abundant nearshore species such as salmon, lingcod, rockfish, Dungeness crab, and others used to be. However, in the absence of major reserves where these large populations can be demonstrated today, most people simply do not realise just how much humans have modified and decreased the relative abundances of virtually all exploited species. Serial depletion of one species after another has too often occurred (e.g., Orensanz et al. 1998; Pauly et al. 1998). Too often, our response following collapse of a fishery is to look for another species to exploit rather than to ask the difficult questions as to how to rebuild and sustain overexploited populations and then implement the answers. Short-term economic needs and political benefits regularly tend to override the much larger, potential long-term benefits that would be obtained from sustainable exploitation of our ecosystems.

Intraspecies genetic and (or) behavioural diversity

Although most marine species are managed as if the exploited population was a single homogeneous "stock unit," it is now widely accepted that many populations of spatially persistent species may consist of a number of discrete adult stocks, or metapopulations. Often, these are populations where the adults do not intermingle but that are connected through meroplanktonic larval dispersal. Specific habitats or ecosystems may favour either the survival of specific genotypes that differ from other populations of the same species or the expression of unique behaviours. However, while studies may have reported that different populations have different behaviours and that observed behaviours are uniquely adapted to local conditions (e.g., Dungeness crab; Jamieson and Phillips 1993), whether they are manifested because of genetic differences or environmental features has invariably not been studied. An exception is with some Australian abalone, where it has been shown that more distantly separated populations are genetically more different from each other (Shepherd and Brown 1993).

The more diverse age structure and genetic base associated with reserves may also reduce the risk of fishery collapse (Roberts et al. 1995; Holland and Braze 1996). Trippel (1995) suggested that reproductive capability and resiliency to environmental fluctuations in heavily fished populations may be reduced as the average age and average age of maturity are reduced. Jamieson et al. (1989) expressed concern that virtually complete harvest in the whole population of the fastest growing portions of crustacean cohorts before they have the opportunity to reproduce may be inadvertently selecting for either slower growing individuals or a lower probability of moulting to the legal size. Although the genetic basis behind growth rates for many species has not yet been studied, a precautionary management approach would ensure that all members of a year-class would have the opportunity to breed. Since this is difficult to achieve in many existing exploited areas, the benefits of having reserves would be that at least a portion of every entire year-class would have a breeding opportunity largely unmodified by fishing activity.

Implications of marine protected areas for conservation

The implications of marine protected areas for marine conservation or fisheries are both complementary and contradictory. Renewable resource conservation through protected areas may imply some probable restriction of human fishing activity but is likely to enhance achievable yields in adjacent exploited areas. In both cases, the relative geographic scales of reserves in comparison with exploited areas and the nature of the protection provided become important and should be related to the objectives that are defined with the establishment of each marine protected area. Here, we separately consider habitat, individual species, and ecosystem, or biodiversity, protection.

Habitat

Apart from the effects of ocean dumping, mineral, oil, and gas extraction, and fishing activity, most marine habitat is unlikely to be negatively physically impacted by humans except in very nearshore areas, where dredging and shoreline modifications, such as dyking, infilling, and pier construction, may occur. Effects of water pollution and sediment runoff are also more acute in the shallower areas. In Canada, habitat and renewable marine resource management are to a large extent the responsibilities of separate departments and ministries within the federal and provincial governments. In the past, DFO has vetted all perturbations that might affect renewable resources but typically has only restricted habitat alterations or deposition of deleterious substances (pollution) if sensitive habitats in potential impacted areas were likely to be directly or indirectly affected. Examples are the high level of protection given to separate habitats, such as seagrass beds, estuarine marshes, or kelp beds, and the concern about dioxins in shellfish. In some instances, DFO is a key stakeholder for the management of large geographic areas, such as the Fraser River estuary, but even here, only productive salmonid habitat is afforded the most protection (see http://www.bieapfremp.org/fvision.htm). Passage of the Oceans Act has broadened this department's mandate, and it is now beginning to proactively identify areas worthy of protection even if exploited species are not obviously at risk. For example, identification of extensive sponge reefs in Queen Charlotte Sound and southern Hecate Strait in B.C. by Conway (1999) has led to internal DFO recommendations that they be protected through MPA designation (Stocker and Pringle 2000). However, as discussed above, the level of protection applied in each MPA is individually considered, so it will not be known what "protection" will actually be applied until each specific designation is finalised.

B.C. has historically been more proactive than the other Canadian coastal provinces in establishing habitat protection through marine protected areas. However, with provincial parks representing most of the areas protected in B.C., protection has primarily been for terrestrial and water surface recreation values (sheltered coves and harbours are well represented) rather than for the intrinsic value per se of the in-

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digenous marine life's habitat. Because most nearshore habitats, being within headlands, are provincially managed, from a conservation perspective, the most complete protection for reserves would result from a collaborative designation of marine protected area status by both provincial and federal levels of government. The participation of DFO is essential, since it alone regulates marine fish habitat and fishing activity and thus the indirect habitat effects arising from fishing.

Sensitive species

Some sedentary species that are relatively fragile to physical impact (e.g., corals, gorgonids, and sponges) are particularly sensitive to human impacts. Other species may be particularly vulnerable to human impacts: (*i*) at different times in their life cycles to fishing (e.g., gillnetting in estuaries for returning salmon) or to particular gear types as bycatch (e.g., rockfish to salmon trolling), (*ii*) if they are relatively rare and localised, even if only for a short time period (e.g., marine bird and pinniped rookeries, spawning abalone, and killer whales at rubbing beaches), or (*iii*) if they are long-lived with relatively low fecundity, such as some whales, sharks, and sturgeon, making them more vulnerable to risk of extinction (Powles et al. 2000). For fragile species that are sedentary, immobile, and long-lived (e.g., corals and reef sponges), ideally, species concentrations would be located and significant areas protected before the population could be seriously impacted. For mobile species that either have to pass through spatial "bottlenecks" in their movements or are frequently caught as bycatch in the targeted fishing of other species, marine protected areas that include areas of particular species vulnerability might provide critical protection to help sustain specific stocks or cohorts. Examples of marine protected areas in Canada established primarily to protect species using specific habitats (protection may be seasonal, i.e., only when the species are present) are MBSs, B.C. ecological reserves (e.g., Robson Bight (Michael Bigg)) for killer whales, B.C. wildlife management areas, and some provincial parks for seabird breeding colonies (e.g., in B.C., Scott Islands and Mitlenatch Island Nature provincial parks).

Biodiversity

With the current move towards an ecosystem-based management approach by DFO, the challenge now is to understand what this actually will mean in an operational sense. Most marine biological communities are poorly described, and while species lists of larger harvested species may be available, their full roles in and contributions to the ecosystems that they occur in are largely speculative. In addition, historically fishers targeted higher trophic level species, which has now disrupted relative species abundances and therefore local ecosystem dynamics. What ecosystems were historically like is now mostly speculation. Marine reserves provide the opportunity for natural ecosystems to become reestablished by permitting exploited populations to achieve their natural size frequency distributions and, if monitored, the research opportunity to determine how exploitation of some species affects the relative abundances and ecosystem roles of other species. This allows evaluation as to whether or not there are keystone species and, if so, what their specific ecological roles are (Power et al. 1996; Miller et al. 1998).

An example is the B.C. gooseneck barnacle (*Pollicipes polymerus*) fishery and its potential impacts on exposed rocky intertidal ecosystem dynamics. Recent reports by Lauzier (1999) and Jamieson et al. (1999) described both fishery and ecosystem concerns, respectively. They discussed the need for reserves and experimental management areas to determine the ecosystem role of this species and that of the sea mussel *Mytilus californianus*, which together are the dominant structural species in this ecosystem. Up to 300 other species are associated with the microhabitat that these two species create, so their harvests, if substantial, may have widespread ecosystem implications. The conservation value of reserves in this ecosystem is now being investigated. With single-species management, population reference points have been accepted for many species. A fishery, for example, might be shut down if the population size decreases to below a specified percentage of an historical average abundance estimate. Studies are now needed to establish comparable ecosystem reference points. If harvest of a species affects the numbers of other species in an ecosystem, or the relative abundances of other species in the ecosystem, then criteria are needed to determine what levels of impacts are acceptable and how impacts should be measured. This is an area of fishery science that has not been intensively studied, yet is one that is now perceived as important, since it is related to the overall sustainability of both ecosystems and fisheries.

As an example, ICES (2000) recently considered the ecosystem effects of fishing activities (beam and otter trawling) in the Northeast Atlantic and proposed a number of priority management measures, including the creation of closed areas. ICES (2000) also considered species abundance thresholds in ecosystems that might inadvertently be crossed. The result might be new, relatively stable, ecosystem equilibria being established, with different species dominating in abundance in each. The slowness in the recovery of Atlantic cod may in part be because of a change in ecosystem dynamics, and it has been postulated (Guénette et al. 2000) that the presence of substantial reserves could have helped sustain cod abundance if they had been in place. These are theoretical analyses, but modelling suggests that with precautionary management, the presence of reserves can be advantageous and reduce the risks of potential ecosystem change. Where broad reviews have been conducted (e.g., Anonymous 1997), effective reserves are felt to increase resource harvest sustainability.

Implications of marine protected areas for fisheries management

The beneficial results of having marine protected areas can best be evaluated by considering the primary species involved and site-specific aspects (Murray et al. 1999), as ecosystems and species are too complex to permit any quantitative generalisations that would be meaningful everywhere. However, there are some general benefits that merit discussion regarding the utility of marine protected areas as a tool in fisheries management. Specifically, we discuss the science need for baseline reference sites, the use of protected areas in experimental management, optimal proportions of coastal areas that might ultimately be protected and still sus-

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tain acceptable fish harvests, and the implications of an marine protected area network.

Baseline, or control, sites

One of the challenges in evaluating the potential of reserves is in a priori determination of what the biological community would be like with minimal human impact. Most marine systems have already been extensively impacted (e.g., Lindeboom 1995; Dayton 1998). However, even if fishing in an area was totally eliminated, some human impacts might still continue to exert effects. These include fishing of mobile species elsewhere, possible upland impacts and discharges into the ocean, the possible movement of pollutants and toxins into the area via currents, and climate change if shown to be an effect of human activity. However, in many areas, the effects of fishing are likely to be the present dominant factor affecting the abundances and size frequency structures of most exploited, relatively sedentary species. Reserves would allow natural trophic levels in the community to reestablish themselves. Some of the larger, typically more mobile species that may have been extirpated from the region, such as some whales, basking sharks (*Cetorhinus maximus*), and sea otters in B.C., may take a relatively long time to reestablish, if they ever do. Thus, the biological system that will reestablish now over the long term may not be quite that of the pristine system, but it would be the most natural system possible at this time.

From a research perspective, having such representative systems available for study has a number of advantages. First, comparative monitoring would allow natural mortality and growth rates of exploited species unbiased by fishing to be estimated. While there may be some site-specific differences for these parameters between reserves and exploited areas, in many cases the consequences from fishing are likely to be most significant. Having unbiased parameter estimates could allow improved evaluation of estimates obtained from exploited areas. The basis behind maximising yields in existing fisheries is that by modifying population size frequency structures, the effects of density dependence can be used to maximise production, i.e., growth and survival of recruiting individuals, so that the harvestable yield is optimised. It is thus important to know how parameters estimated in fished environments have actually been modified by fishing. Second, estimates of potential population fecundity are difficult to predict from a significantly modified population size, or age, structure, and while such a natural structure can be postulated, having actual data from unharvested populations would again be desirable to evaluate predictions against.

Experimental management

Theoretical analyses (e.g., Hastings and Botsford 1999; Sladeck Nowlis 2000) and a few field studies (e.g., Alcala and Russ 1990; Bennett and Attwood 1991) suggest that reserves can increase yield with spatially persistent species. Additional field evidence within Canada would be desirable to show fishers that this is indeed the case. However, a problem is that as reserves begin to be established, the full potential of reserves as a stock management tool may not become evident until fishing is terminated over a significantly large amount of the total exploitable area, i.e., until the collective benefits of a reserve network have been established. There is thus the danger that evaluations of field data may be made either too soon or on the basis of inadequate reserve area to allow their full benefits to be evaluated. In the absence of functional reserves that restrict fishing in Canada, the benefits of having a variety of sizes of marine reserves protected may only be assessable theoretically. Only through actually protecting areas can actual benefits and costs be accurately determined and the concerns of cynics as to the merits of reserves be best addressed. Adaptive management (Walters 1986) needs to be accepted as the desirable way of managing a resource. A monitored experimental manipulation of the benefits of having different-sized areas closed to all fishing for specific species has not been attempted to date, so trials that would do this would be "experimental management." Ongoing monitoring of population responses for relevant species is required at an appropriate time scale, since restrictions on fishing that might be imposed should be adjustable over time so that closures with optimal characteristics can ultimately be identified.

Optimal proportion of the coast in reserves

Politics are to a large extent the balancing of different human interests against each other, and as the marine environment becomes more extensively utilised by humans, the politics of how the marine environment will be used become more complex. In balancing options, there is often the assumption by managers that if areal allocations are approximately equal within an arbitrary accepted harvest level, then they are probably fair. However, while this assumption may generally apply to opportunities for accumulation of monetary wealth, its application to biological systems is not based on science and is not likely to ensure sustainability over the long term. Fairness has nothing to do with the realities of habitat availability, relative species abundances, and so on. "Protection" in reserves of a relatively low (e.g., 10–20%) arbitrary overall percentage of an area with many diverse habitats is likely to be ecologically unsound if the sustainability of a diversity of renewable resources is a primary objective. Some species may benefit, but since protection of the most productive areas is likely to be most resisted by existing users of these areas, the result may tend to be excessive protection of the least productive areas and minimal protection of the most productive areas. Protection is thus not likely to be truly representative of the actual diversity of habitats that exists unless particular efforts are made to achieve comparable protection of all habitats.

Strong science arguments as to the benefits of an optimal level of protection in reserves for significant amounts of all habitats are required. The effectiveness of reserves is some function of reserve size (Edgar and Barrett 1999), and reserve size needs to be judged against the objectives identified. Theoretical studies are needed to evaluate how the productivity of habitat is related to the benefits that might be achieved through reserves. The protection of highly productive areas may suggest that less overall area would need protection while still achieving the benefits associated with reserves. However, minimising the area protected may not be commensurate with maximising benefits and should not necessarily be substituted as a surrogate goal.

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The benefit arising for many species from having a relatively large proportion (e.g., ≥40%) of the marine environment in reserves is a hedge against overexploitation by fisheries (Clark 1996; Sladeck Nowlis and Roberts 1999). Results are related to assumptions around larval transfer functions between reserves and exploited areas. However, it must be recognised that connectivity in the marine environment differs significantly from that in the terrestrial environment (Jamieson and Levings 1998). Connectivity between populations may also largely be a function of habitat type, with species from reef habitats likely to be more sedentary than those inhabiting flatter bottom habitats. The latter habitats are more homogenous, and so, individuals in them are likely to be more wide ranging. The dispersal of most species through meroplanktonic larvae and the open nature of most water bodies means that high harvest rates may be sustained in exploited areas if sufficient reproductive refugia are maintained to provide the exploited area with sufficient larvae for the habitat's carrying capacity for that species.

As a consequence, some marine conservationists have proposed protecting in reserves a specific percentage (e.g., 20% of the area for Atlantic reef fish (Bohnsack 1990) and 10% of all marine habitats in New Zealand (Ballantine 1991)) of the marine environment. This concept is controversial in the terrestrial environment (e.g., 12% is the government's protected area goal for terrestrial B.C.), where it is being questioned by conservationists, and we suggest that it is an even less appropriate concept for the marine environment. The recent petition by many scientists to the world's leaders to set aside in reserves the minimal value of 20% (e.g., U.S. Coral Reef Task Force 2000) is admirable but runs the risk of having insufficient productive or important areas protected to achieve the results expected. However, many environmentalists felt that having something significant protected, at least initially, was better than possibly having relatively little protected and that the time was right to make this argument. However, the devil is often in the details. Without any clear assurance as to what areas might comprise the protected 20%, there is a substantial risk that while that goal may be met, the twin objectives of having all habitats adequately conserved and all existing fisheries sustained may not be. If an appropriate conservation percentage were applied to all a region's major consensually defined marine habitats, then the merits of using a percentage value as a good starting point may be more justifiable. However, the logistics of doing this may be relatively difficult to effect.

Marine protected area networks

Having an adequate prior understanding of at least some of the factors affecting dispersal of the targeted species would seem to be a requirement to develop an optimal network of reserves for species enhancement and the sustenance of fisheries. If metapopulations are known, or are assumed, to exist, it is ideally important to know whether the area where a reserve is being proposed has source or sink populations (Pulliam 1988; Roberts 1998). Sources are areas that contribute disproportionately large quantities of recruits, i.e., larvae and juveniles that survive to reproduce, to future generations, whereas sinks are areas that receive recruits but contribute little to future generations. However, such knowledge is known for only a few species worldwide, and the point has been made (Roberts 1998) that attempting to identify sources and sinks a priori will needlessly delay the establishment of reserves and so oppose rational resource management. Also, different species may have different source and sink areas, so no one reserve is ever likely to be ideal for all species. B. Ballantine (in Pitcher 1997) stated that when little is protected in the early stages of the development of a network of reserves, it does not make too much difference in the long run which area is first protected. Roberts (1998) agreed and stated that the surest way to achieve fishery and conservation goals is to establish a dense network of reserves that incorporate a wide variety of habitats and locations, since then at least some source areas are likely protected by reserves.

Networks also require consideration of the areal scales of the individual reserves involved — should there be a few large or many small reserves? This issue has been discussed under the SLOSS (single large or several small) debate mostly for terrestrial situations. With connectivity issues so different in the marine environment (Jamieson and Levings 1998), its applicability in the marine environment is less certain and has been less studied. McNeill and Fairweather (1993) described an experimental evaluation of this issue, and while they obtained inconclusive results, they did emphasise that processes affecting species' recruitment and the suggested importance of a fragmented habitat on recruitment need particular consideration. Study of how pattern and variability change with the scale of description becomes an important factor (Levin 1992; Dutton and Saenger 1994), as does the mobility of species. The species most likely to disappear from small reserves are those that range most widely, irrespective of population size (Woodroffe and Ginsberg 1998).

Qualitative scheme for classifying and categorising marine protected areas by "level of protection"

Given the variety of marine protected area designations and the different restrictions of human activity associated with each designation type, we believe that there is value in having a relatively objective method of comparing different marine protected area designations by the relative levels of protection that each designation type implies. We therefore propose a process by which this may be done.

We categorise protection with regards to both habitat and (or) species and consider the nature of protection offered by legislation rather than the broad types of impacts that might actually be occurring. Because the nature of impacts can be quite variable, we have considered impact effects in three ways: their severity, duration, and extent. Severity was the relative degree of harm or destruction, without consideration of duration or geographical extent, and was low, medium, or high. An example of a low impact would be disturbance arising from anchoring. Weight is put on the sea floor and the substrate may even be slowly disturbed if the anchor drags, but since anchoring in most coastal areas is by vessels <20 m in length in waters with no significant biological structure (macrophytes or corals), little species mortality typically arises. An example of a high impact would be complete

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Table 4. Impacts and their proposed relative weightings for different human activities on habitat and species.

General activity	Specific activity	Extent of impact (0 = least, 10 = greatest) Direct	Indirect
Habitat impacts			
Resource extraction	Mineral extraction	5	7
	Oil and gas	3	7 (accidents)
	Gravel and sand	5	7 (sediment plume)
Effluent discharge	Industrial or domestic outfall	3 (if diluted adequately)	7 (sublethal effects may promote toxic blooms)
Ocean dumping	Dredged material (may include wood)	5	4 (possible toxics)
	Garbage	5	4 (possible toxics)
	Rock and soil	5	4 (sediment plume)
Dredging	Channels	5	4 (sediment plume)
	Loading areas and terminals	2	4 (sediment plume)
Construction	Piers and docks (piling)	2	2
	Piers and docks (infill)	2	2
Land reclamation	Dyking	10	8
	Groins and breakwaters	2	5 (accretion and erosion)
	Sea walls	2	5 (erosion)
Anchoring		2	2
Fishing	Trawling	8	7
	Longlines	8	5
	Intertidal clam digging or algae harvest	2	2
Aquaculture	Suspended	1	2
	Fish net pens	5	4 (possible toxics)
Ballast water dumping	Introduction of structural species (e.g., mussels and algae)	1	2
Upland disturbances	Increased sedimentation discharge	2	1
	Reduced freshwater discharge	3	2
	Disturbance of natural vegetation	2	1
Logbooming		4	2
Species impacts			
Fishing (managed)	Trawling	8	0
	Longlining	4	0
	Single-pot trapping, diving, gillnetting, pole fishing, etc.	4	0
	Marine plant harvest	2	0
Fishing (unmanaged)		10	0
Aquaculture	Benthic shellfish	3	0
	Intertidal poles	1	0
	Suspended (bivalves, plants)	1	0
	Fish net pens	3	3 (waste and chemical dispersion)
Hunting		3	2 (disturbance)
Behaviour disturbance	Any human activity, including tourism	4	3

Note: Relative "level of protection" would be the sum for those habitat and species impacting activities that are specifically excluded by legislation. *w*,

habitat destruction by dredging or ocean dumping. Duration was the estimated time from the initial stress to recovery and was short term (<2 years), medium term (2–15 years), or long term (>15 years). Extent was the geographical extent of the impact and was site specific, local, or regional. We then considered both the direct and the indirect effects of each activity, with the total score for the impact of each activity the sum of the direct impacts plus a variable proportion (0.1–0.5) of the indirect impacts. We have tried to include all the potential impacting activities that may occur at any site, but additional ones can be added as needed. The scoring that we propose was developed by us and then modified by comments from a number of recognised regional experts (Delphic approach; Crosby et al. 1997 (see Acknowledgements)).

Relative "level of protection," which we term the "protection coefficient" (PC), for each designation type is the sum for those habitat and species impacting activities that are specifically excluded by legislation. The higher the cumulative value of the total excluded impacts, i.e., the PC, the

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Severity and duration of impact (0 = least; 10 = greatest)		Impact (Σ direct) + ($w \times \Sigma$ indirect)		
Direct	Indirect	w = 0.1	w = 0.3	w = 0.5
10	8	16.5	19.5	22.5
3	8 (accidents)	7.5	10.5	13.5
10	8 (sediment plume)	16.5	19.5	22.5
3	7	7.4	10.2	13
10	4 (possible toxics)	15.8	17.4	19
10	4 (possible toxics)	15.8	17.4	19
10	6 (sediment plume)	16	18	20
10	6 (sediment plume)	16	18	20
10	6 (sediment plume)	13	15	17
2	2 (fishing and litter)	2.4	3.2	4
10	5 (modified currents, fishing, and litter)	12.7	14.1	15.5
10	8 (removal of estuarine or intertidal habitat)	21.6	24.8	28
10	6	13.1	15.3	17.5
2	4	4.9	6.7	8.5
1	2 (fishing and litter)	3.4	4.2	5
8 (destruction of substrate structure or structural, epibenthic species, e.g., corals)	4 (sediment plume; loss of habitat for other species)	17.1	19.3	21.5
3 (destruction of structural, epibenthic species, e.g., corals)	3 (loss of habitat for other species)	11.8	14.4	15
2	2	4.4	5.2	6
1	2	2.4	3.2	4
9 (destruction of benthic species)	6 (possible toxics)	15	17	19
1	2	2.4	3.2	4
2	1	4.2	4.6	5
5 (disruption of estuarine functions)	3	8.5	9.5	10.5
2 (removal of detrital sources)	2	4.3	4.9	5.5
8 (smothering with bark debris, anoxia)	2	12.4	13.2	14
8 (biological community disruption)	4 (bycatch)	16.4	17.2	18
6	3 (bycatch)	10.3	10.9	11.5
4	2 (bycatch)	8.2	8.6	9
4	2 (bycatch)	6.2	6.6	7
8 (biological community disruption)	4 (bycatch)	18.4	19.2	20
4	3 (predator control)	7.3	7.9	8.5
1	2 (predator control)	2.2	2.6	3
0	0	1	1	1
0	4 (waste and chemical dispersion; potential exotic species escapes)	3.7	5.1	6.5
4	3 (disturbance)	7.5	8.5	9.5
0	4 (site avoidance; reduced feeding and reproduction opportunities)	4.7	6.1	7.5

weighting value.

more the marine protected area is generally protected. We gave indirect impacts an arbitrarily range of reduced weightings (0.1–0.5) relative to direct impacts (Table 4), but while this changed the overall magnitude of the PC calculated, it did not change the relative rankings of overall protection by marine protected area type. Here, we evaluate PCs for marine protected areas in B.C. only, as we did not have details of the legislations under which other provincial and territorial marine protected areas were established in Canada. Environment Canada's national wildlife areas had the highest score, followed by a tied score between national parks and B.C.'s ecological reserves (Table 5). B.C.'s provincial parks and wildlife management areas ranked quite well, with Environment Canada's MBSs ranking quite low. Most of these protected area types, however, did not restrict fishing, which is the single activity that many people associate with a high degree of marine resource protection. As a specific impact, the habitat score associated with fishing is similar to other individual habitat impact scores (e.g., resource extraction). However, because there is also a species impact score

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Table 5. Examples of protection coefficient (PC) values for marine protected areas in B.C.

Jurisdiction	Marine protected area type	Excluded human activities	Habitat PC value (w = 0.5)	Species PC value (w = 0.5)	Total PC value		
					w = 0.1	w = 0.3	w = 0.5
B.C.	Ecological reserve[a]	Resource extraction Ocean dumping Dredging Land reclamation Logbooming Aquaculture Hunting Behaviour disturbance	244.5	36	212.9	246.7	280.5
	Provincial park[a]	Resource extraction Ocean dumping Dredging Land reclamation Log booming Aquaculture	244.5	19	200.7	232.1	263.5
	Wildlife management area[b]	Resource extraction (only sand and gravel) Ocean dumping Dredging Land reclamation Log booming	185.5	0	145.1	165.3	185.5
	Designated wildlife reserve[a]		0	0			0
	"Protected" area[a]		0	0			0
Federal	Marine protected area[c]		0	0			0
	National wildlife area[a]	Resource extraction Ocean dumping Dredging Land reclamation Logbooming Fishing Aquaculture Hunting Behaviour disturbance	287	101.5	305.7	348.1	388.5
	Migratory bird sanctuary[a]	Hunting (seasonal) Behaviour disturbance (seasonal)	0	17	12.2	14.6	17
	National park[a]	Resource extraction Ocean dumping Dredging Land reclamation Logbooming Aquaculture Hunting Behaviour disturbance	244.5	36	212.9	246.7	280.5
	National marine conservation area[c]		0	0			0

Note: Data partially derived from Jamieson and Lessard (2000). w, weighting value.

[a]Generic activities excluded through an Act and therefore characteristic of all marine protected areas of this type.

[b]Only activities compatible with wildlife management are permitted, and so while an Act may not specifically exclude many activities, interpretation of the Act by the site's managing director would preclude the occurrences of activities negatively impacting habitat.

[c]There are no specific human activities excluded through the relevant Act itself, with specific restricted activities determined on a site-by-site basis and then established through regulation. However, fish habitat alteration and disruption and deposition of a deleterious substance are prohibited under the Fisheries Act (see What does "protected" mean? section).

associated with this activity, fishing does in fact have a proportionately high protection value associated with its exclusion from a protected area. Because restrictions for some marine protected area designations are determined on a site-by-site basis (e.g., DFO's MPAs and Parks Canada's NMCAs), theoretically anything can be protected, but no specific thing

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is always protected. Individual sites of these marine protected area types, when established, may potentially rank quite high, but generically, the designation type ranks low, as no protection of any kind is assured.

Future literature may use different relative impact scores or weightings, but if any such changes are described, reference in the literature to relative rankings of marine protected areas proposed here can be compared. At the least, we hope that this evaluation will provoke discussion and recognition as to the actual protection associated with the different types of protected area designations.

The exclusion of fishing by fishery closures for a few individual species in specific marine protected areas has also not been included here as a measure of protection, since such restrictions can be changed relatively easily by regional authorities through variation orders. Existing fishing restrictions may not necessarily be maintained over time scales meaningful for protection of longer lived (50+ years) species in particular, such as rockfish and some shellfish.

This proposed ranking approach has the implementation advantage of only needing to know those impacts that legislation excludes rather than all the possible impacts that may actually be occurring. By comparing the actual impact values for different activities, it is possible to compare the impacts of quite different activities, or even pairs of impacts such as land reclamation and trawling or liquid sewage discharge and dredging. With this proposed approach, different marine protected areas can therefore be evaluated in a number of ways. These include the level of relative protection offered for either habitat or species, or for both combined, and the level of impacts for activities that are known to be occurring, again for either habitat or species or for both combined.

Finally, we have not considered the time period during which the legislated protection may have been in existence for specific sites, even though this may be a crude measure of whether the local environment is now once again relatively pristine. Duration of past protection is too dependent on site-specific information. Factors important here are the species involved and their biologies, the environmental conditions that they occur in, the relative size of the protected area, and a host of other non-marine protected area considerations, including continuing upland impacts, transport of pollutants from outside the area into it, and so on.

Conclusions

The conceptual value of and need for marine protected areas are now well established and broadly accepted by both resource managers and the general public in Canada and in most areas of the world. Nevertheless, many fishers still have concerns that restrictions on fishing will affect their economic incomes. This issue will only likely be adequately addressed through documentation of the consequences in established protected areas, as while theoretical studies may suggest sustainable yields, documented evidence is the best persuader. The beginnings of a coordinated approach to human activity restrictions within protected areas by both the provincial and federal governments are now underway in Canada. However, these efforts to date, at least in B.C., are only just beginning to result in effective renewable marine resource protection through marine protected areas. Difficulties here are a lack of understanding and appreciation as to what might result from use of the different legislative tools available for establishing marine protection and concern that any government restriction of ongoing harvesting will have negative economic consequences. The first MPA in Canada, XwaYeN (Race Rocks) MPA, is a 251-ha no-harvest MPA whose boundaries will exactly match the existing B.C. Race Rocks Ecological Reserve. For renewable resource conservation in other areas, the primary management tool remains fishery closure regulations, quotas, and other traditional stock management measures. In Canada, a process to broaden the establishment of Oceans Act MPAs beyond the five candidate MPAs announced in 1998 is still being developed. Obtaining support from all relevant sectors (First Nations, commercial and recreational fishers, and other resource users) is an important component.

Nomenclature is an issue that needs special attention, as there remains much ambiguity around the use of names (parks, reserves, sanctuaries, etc.) to describe the various areas where protection has been claimed. Provinces establishing protection do not have the mandate or resources to effect protection of renewable marine resources, which the general public would expect from the designated name. In part to address this concern, we proposed a quantitative approach for ranking marine protected areas based on the defined restrictions in the Acts under which they were legislated. Environment Canada's national wildlife area designation offers the most protection, followed by a tied score for National Parks' and B.C.'s ecological reserves. However, as we pointed out, having restrictions designated as laws is separate from having laws enforced, and illegal harvests are a problem everywhere if only enforcement officers monitor human activity. Support and ongoing monitoring by people in local communities are essential if real protection is to be provided in any protected area, whether on land or in the water. This realisation is why so much effort is currently being devoted to obtaining community consensus for boundaries and levels of protection within candidate and existing marine protected areas and why the process of establishing functional marine protected areas has become so time-consuming. It is a complex challenge, one that only time and a will to ultimately succeed can address.

Actual no-take areas of sufficient number, size, and scale to offer functionally significant marine ecosystem protection are almost nonexistent in Canada. Consequently, there are inadequate Canadian field studies of the full benefits that might be obtainable from such reserves, although there have been a number of theoretical analyses. Long-term assessment of the effectiveness of protected areas in meeting conservation or fisheries objectives is required. This should involve (*i*) some ongoing monitoring of biodiversity and the abundances of targeted species, (*ii*) examination of geographical scale relationships of biogeographic assemblages against those of protected areas, (*iii*) evaluation of the functional role(s) of conserved species within the protected ecosystem, and (*iv*) evaluation of relevant dynamic hierarchical relationships and feedbacks among relevant marine ecosystems. None of these are trivial tasks, but if a scientific analysis of the performance of marine protected areas in meeting defined objectives is desired, then consideration of the above is required.

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What controls who is where in freshwater fish communities — the roles of biotic, abiotic, and spatial factors[1]

Donald A. Jackson, Pedro R. Peres-Neto, and Julian D. Olden

Abstract: We examine evidence for the structuring of fish communities from stream and lake systems and the roles of biotic, abiotic, and spatial factors in determining the species composition. Piscivory by fish is a dominant factor in both stream and lake systems whereas evidence for the importance of competition appears less convincing. Within small streams or lakes, the impact of predation may exclude other species, thereby leading to mutually exclusive distributions and strong differences in community composition. Within a geographic region, abiotic effects frequently dictate the relative importance of piscivory, thereby indirectly influencing the composition of prey species present. The spatial scale of studies influences our perceived importance of biotic versus abiotic factors, with small-scale studies indicating a greater importance of competition and large-scale studies emphasizing abiotic controls. The scale of the individual sites considered is critical because smaller systems have higher variability and wider extremes of conditions than larger lakes and rivers. The stability of physical systems and degree of spatial connectivity contribute to increased diversity in both larger stream and larger lake systems. We identify challenges and needs that must be addressed both to advance the field of fish community ecology and to face the problems associated with human-induced changes.

Résumé : Nous avons étudié la structuration des communautés de poissons dans les cours d'eau et les lacs, ainsi que le rôle des facteurs abiotiques, biotiques et spatiaux dans la détermination de la composition spécifique. La piscivorie par les poissons s'avère être un facteur dominant, tant dans les cours d'eau que dans les lacs; en revanche, le rôle de la compétition est établi de façon moins convaincante. Dans les petits cours d'eau et lacs, la prédation peut exclure des espèces, ce qui résulte en des répartitions mutuellement exclusives et de fortes différences dans la composition des communautés. Dans une même région géographique, les facteurs abiotiques contrôlent souvent l'importance relative de la piscivorie, influençant ainsi la composition spécifique des proies présentes. L'échelle spatiale à laquelle les études sont conduites affecte la perception que l'on peut avoir de l'importance relative des facteurs biotiques par rapport aux facteurs abiotiques; les études à petite échelle révèlent une plus grande importance de la compétition, alors que celles à grande échelle mettent de l'avant les facteurs de contrôle abiotiques. L'échelle spatiale des sites individuels choisis revêt une importance critique, parce que les systèmes plus petits sont plus variables et présentent un plus grand éventail de conditions extrêmes que les grands lacs et les rivières. La stabilité des systèmes physiques et le degré de connectivité spatiale entraînent un accroissement de la diversité, tant dans les rivières que les lacs de grande taille. Nous identifions, en terminant, des défis à rencontrer et des besoins à combler pour faire progresser l'écologie des communautés de poissons et pour pouvoir faire face aux problèmes causés par les changements anthropiques.

[Traduit par la Rédaction]

Introduction

Ecological communities and the study of their structuring factors have a long, rich history. Studies focused on terrestrial systems stimulated some of the initial and heated debates about whether or not communities contain discrete and nonrandom assemblages (e.g., Connor and Simberloff 1979) and whether species, and therefore communities, are regulated by biotic or abiotic factors (e.g., Andrewartha and Birch 1954). In many of these cases, aquatic community ecologists have joined into these debates subsequently, yet have not initiated the research and theory. However, other topics have demonstrated the leadership of aquatic ecologists. For example, in general, aquatic ecologists have accepted the view of ecosystem-level factors in determining species composition for a longer period of time. Because shoreline boundaries of lakes and rivers were perceived as limiting the potential for movements and dispersal by aquatic organisms, early ecologists focused on the factors operating within each individual system in a more holistic

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manner than terrestrial ecologists, who placed more emphasis on dispersal and colonization to influence species abundance and composition. During the last two decades, we have seen a convergence of these ideas, with terrestrial ecologists placing greater emphasis on ecosystem-level processes than in the past and aquatic ecologists viewing these boundaries as being less discrete. Studies of movements of aquatic organisms (fish, zooplankton, mollusks), whether accidental introductions of exotics, the stocking of fish to new locations, or the natural movements of such species between systems, have shown that the scale at which much of our research has been conducted may need to be expanded. A great deal of the aquatic research has focused on freshwater fish communities, our topic as well, undoubtedly due to their economical and societal importance.

Our first goal in this paper is to provide a snapshot of important findings and generalizations regarding the role of biotic and abiotic factors in regulating fish communities of stream and lake systems. We summarize the field's progression and our current understanding, ideas, and research approaches. We limit ourselves to particular sets of factors that have been identified as important in multiple studies or that we view as particularly promising. Space limitations require us to focus on major sets of factors and omit others that we consider to be less important across studies, although they may be important in specific cases. We attempt to remedy this limitation by directing the reader to associated studies that provide more detail on these topics (e.g., Matthews 1998). However, prior to this summary, we must address the ways of classifying fish communities and whether communities represent anything other than random sets of species sampled at particular locations and times. If they do not, then further analysis may be a fruitless exercise. Our second goal is to examine how spatial arrangements of systems affect fish community composition and how the perceived importance of various biotic and abiotic conditions depends on the spatial scale considered. Finally, we single out what we believe are promising avenues of research or needs for research that can provide major advances in our field. In contrast with most other studies which focus on either lake or stream communities, we seek to identify similarities or differences between the two types of systems, as these should aid in stimulating additional research avenues.

Fish communities: do they really exist, and if so, how do we classify them?

Fish communities are described or classified in various ways reflecting the goals of the study, attributes to be emphasized, and the degree of quantitative analysis employed. In some cases, communities or species assemblages have been named on the basis of ecological and numerical dominance of a particular species or group of species that are of economic value (e.g., Ryder and Kerr 1978). This approach is particularly convenient for resource managers, as the identified species are generally those of management interest. Lake fish assemblages have been designated using this approach or in a more quantitative manner (e.g., Johnson et al. 1977). Similar approaches exist within stream fish community analysis (e.g., Echelle et al. 1972).

Another approach to community analysis has been to classify species into guilds, i.e., species sharing attributes, generally based on feeding or reproduction. This approach is convenient and useful due to its functional nature, as it focuses on specific ecological attributes of the species. Feeding or trophic guilds classify species based on their diet or manner of feeding (e.g., Keenleyside 1979). For species with restricted and consistent diets, this works well. However, many fishes vary their diets as a consequence of ontogeny or opportunity, and a feeding-guild classification needs to be flexible to accommodate the fact that a species may switch between guilds as it grows from a fry to an adult. Individual species may need to be classified into several guilds, thereby complicating the desired use of a simple guild-based approach. However, the explicit recognition of ecological attributes and level of data reduction provided by the guild approach has some appeal.

An additional approach to community classification is through the use of multivariate statistical methods. Although the use of multivariate methods to summarize community patterns began in the early 1900s, their application to fish community analysis is more recent. Some of the first applications to fishes were those by Smith and Powell (1971) and Harvey (1975). Researchers were motivated by the idea that multivariate approaches provided an objective approach in identifying patterns in species assemblages and their relationships with environmental conditions. Since the initial use of multivariate approaches with fish communities, we have advanced in developing and applying methods to predict the assemblages (e.g., Magnuson et al. 1998), to test the association between communities and environmental conditions in lakes (e.g., Jackson and Harvey 1993) and rivers (e.g., Taylor et al. 1993), to measure and remove the role of spatial autocorrelation (e.g., Mandrak 1995), and to assess the importance of isolation (e.g., Olden et al. 2001).

When studying fish communities, researchers make the implicit assumption that the associations of species arise from either biotic or abiotic factors or some combination of the two. However, if the communities are indeed random (i.e., local fauna are composed of random sets of species from the regional pool), then there is little point in studying them in detail because derived patterns may be meaningless. So what evidence exists supporting the hypothesis that fish communities are actually nonrandom in their structure (see Evans et al. (1987) for additional discussion)? One would like to assume that relationships from analyses of communities or community–environment relationships indicate that communities are nonrandom, but this is not necessarily the case because such "interpretable patterns" can be derived from random data too (Jackson 1997). Consequently, we need to consider evidence from studies that specifically test whether or not communities show nonrandom patterns in time and (or) space. The assessment of whether stream fish communities are random or structured (alternatively, stochastic or deterministic) was the focus of a series of papers in the 1980s (Grossman et al. 1982; Yant et al. 1984). This exchange of papers suggested that numerically dominant species often showed consistent patterns over time but that rare species varied greatly, and patterns of rank abundance were also complicated due to seasonal species movements. These findings provided evidence that the timing and extent of sampling may be important factors affecting our perception of stream fish community structure. The spatial and

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temporal scales involved may be important given that variability in species composition and environmental conditions may have different scales (Ross et al. 1985). Finally, the resolution or scale of the data used in such analyses may also influence our conclusions. Rahel (1990) showed that differences in our interpretation may occur depending on whether species relative abundance, rank abundance, or presence–absence data (a quantitative scale issue) are used as the measure of community composition.

Jackson et al. (1992), in a comparison of null models, showed that the fish communities in lakes from each of five different regions were all structured nonrandomly in space. Several studies have recently examined the question of whether fish communities demonstrate concordance with other ecological communities. If two or more communities based on different taxonomic groups show concordant patterns across a range of sites, one can be more confident that the patterns are nonrandom. Example studies have used fish and benthic invertebrate communities from lakes (Jackson and Harvey 1993) and streams (Kilgour and Barton 1999) to show the concordance in these communities across the various locations. These findings support the idea that various fish communities show nonrandom patterns in composition over time and (or) space. We do not know whether this is a general finding for lakes and streams due to the limited number of published studies; however, the studies available do suggest that fish communities are highly structured. In addition, the fact that many studies show similar relationships between particular assemblages and their surrounding environment (e.g., stream flow, lake winter oxygen) provides additional evidence for nonrandom structuring of fish communities.

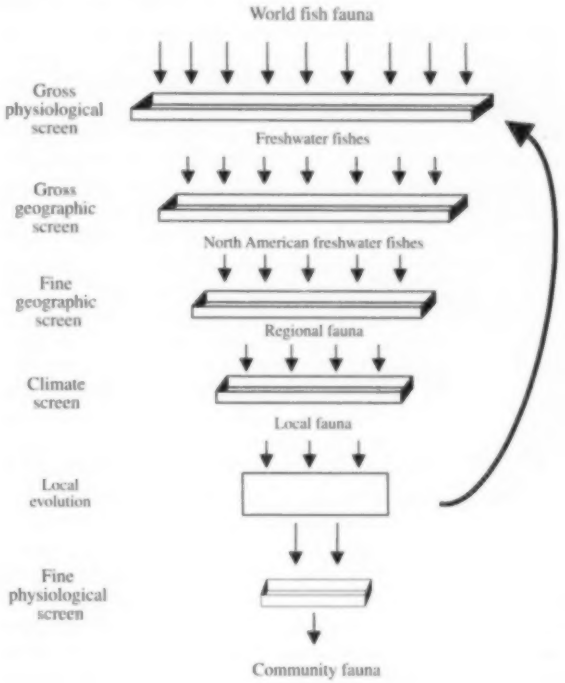
The interaction between issues of scale and the roles of biotic and abiotic factors in structuring fish communities is recognized. Smith and Powell (1971) proposed that the local fish community is the result of a series of selective pressures ranging from geographical effects (e.g., vicariant events) to physiological effects. They proposed a series of screens or filters removing species from the global fauna until only the species found at a particular site remained (Fig. 1). They favored an autecological structuring of the local community that was consistent with the importance that they attributed to abiotic conditions. Jackson and Harvey (1989) and Tonn (1990) proposed similar views regarding this hierarchical nature of factors and scale but placed increased emphasis on the role of biotic interactions, specifically predation, in addition to abiotic factors. We stress that although we structure our paper into sections examining each of these components, there are strong interactions among these three components, and recognition of these interactions is critical in examining virtually any freshwater fish community.

Biotic factors structuring fish communities

Predation

Predation has been shown to have very strong effects on fish communities via direct and indirect mechanisms. Various studies of lake communities have shown the strong and rapid effects imposed by predators, with much of the evidence coming from studies related to species introductions (e.g., Li and Moyle 1981). While the changes in a few lakes

Fig. 1. Selective filtering of the global fish fauna into the set of species comprising the local community within a lake or stream. This is an adaptation redrawn from the hierarchical screening provided by Smith and Powell (1971).



have been followed over time, e.g., the Nile perch (*Lates niloticus*) impact on the Lake Victoria cichlid fauna, other evidence demonstrates the impact of predatory species on communities. Studies by Jackson et al. (1992), Chapleau et al. (1997), and others have shown that many species of small-bodied fishes do not coexist in small temperate lakes where piscivorous species, such as northern pike (*Esox lucius*) or bass (smallmouth (*Micropterus dolomieu*), largemouth (*Micropterus salmoides*)), are present. Cyprinid assemblages show strong negative associations with these predators, and one generally finds either predatory species or the prey assemblage in these small lakes but not both groups. Habitat complexity has been shown to strongly influence the viability of prey populations under predation risk (e.g., Everett and Ruiz 1993), whereas other studies have shown that some species remain vulnerable regardless of the habitat available in small lakes (e.g., MacRae and Jackson 2001). Without these refugia, the prey species may become extinct locally. However, as the size of the lake considered exceeds 150–200 ha in surface area, there is a general trend for both groups to coexist in lakes (D.A. Jackson, unpublished data), likely due to increased habitat heterogeneity and inherent spatial components in the population dynamics of the various species that are not found in the smaller lakes.

Stream-based studies have shown strong predation effects (see Gilliam and Fraser 2001 and references therein). Power et al. (1985) and numerous other studies have shown that predators can affect the choice of habitat by prey species within streams. This may lead to different assemblages be-

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ing present in particular pools or riffles because prey species move to sites providing less risk of predation (e.g., Gilliam and Fraser 2001). Prey species may move to areas where predators have difficulty in accessing them (e.g., Schlosser and Angermeier 1990), and these may be habitats different from those selected when predators are not present (e.g., piranha's (*Pygocentrus notatus*) effect on other species; Winemiller 1989). Gorman (1988) suggested that some of the structure attributed to stream fish assemblages is due to prey species' common avoidance of predators, i.e., species collectively congregating in habitats affording greater protection from predation.

While direct predation effects are often expressed strongly and quickly by the elimination of one or more prey species in the lake or stream system, there are additional, but less obvious, indirect effects by which predators may structure fish communities. When prey species alter their choice of habitat and foraging to reduce predation risk, they may experience corresponding changes in life history and fitness reduction. Slower growth generally means that the individual and species remain vulnerable to predation for a longer time. Fecundity may be reduced if individuals mature at a smaller size, and individuals in poorer condition may experience increased mortality during environmentally stressful periods. For example, Shuter et al. (1980) showed size-selective mortality in the overwinter survival of smallmouth bass. Therefore, predator avoidance may contribute to reduced growth that may be sufficient to prevent successful survival through the winter, thereby preventing the successful long-term survival of the species within such systems. Although the direct effect of smallmouth bass on cyprinids has been discussed, predation can lead to indirect biotic effects through competition. Vander Zanden et al. (1999) showed changes in the diet of lake trout (*Salvelinus namaycush*) as a consequence of bass being introduced into lakes. The bass reduced the availability of the littoral forage base, leading to a reduction in the quality of the trout diets, potentially with life history consequences. Differences in the efficiencies of predators can contribute to changes in the communities (Matthews et al. 1994), particularly when more effective predators are introduced into either lake or stream systems. An example is where a particular assemblage of cyprinids may coexist with salmonid predators, but the diversity of cyprinids is reduced following the introduction of bass into the lakes (MacRae and Jackson 2001). The difference in the cyprinid assemblage response is because the salmonid species are less effective littoral predators than the bass in these lakes.

Predation effects can arise through reduced or enhanced changes in the rates of movements of species between habitat patches. Emigration will hasten the reduction of the population size of prey species by adding to the losses due to direct predation on individuals. Enhanced emigration due to the presence of predators has been shown in lakes (He and Kitchell 1990). However, this is not always the case, as other studies have shown both increased and decreased rates of movements (e.g., Gilliam and Fraser 2001 and studies cited therein). Changes in rates of movement can alter the metapopulation dynamics of fish communities within watersheds encompassing various tributaries or sets of lakes, with the consequences dependent on the spatial arrangements of the water bodies and their connectivity (discussed below).

Experimental studies confirm that the impact by predators is swift and considerable (He and Kitchell 1990). Prey species move into shallow waters, frequent complex habitats, or leave the site to avoid predators (He and Kitchell 1990). Size-selective predation (Wahl and Stein 1989) has been shown to have a strong influence on which individuals and species survive, thereby leading to potentially different communities depending on the presence of particular predators, i.e., those selecting only small-bodied prey species versus those feeding on all species. An important feature identified by Matthews (1998) is that despite the large number of potential predator–prey combinations (e.g., about 900 species of fish in North America), most studies have been limited to examining only a few predators (e.g., largemouth bass, smallmouth bass, creek chub (*Semotilus atromaculatus*)) and prey (e.g., small creek chub, fathead minnow (*Pimephales promelas*), northern redbelly dace (*Phoxinus eos*)). Consequently, the current ideas and theories related to fish predator–prey relationships are based on a limited range of potential species combinations, and comparisons incorporating other groups of species will be helpful.

Competition

Although there is no consensus regarding the role of interspecific competition in structuring stream and lake fish communities, the ample literature associated with resource partitioning among fishes suggests that competition may play an important role in the local organization of communities (see Ross 1986). Most studies are based on field observations, and many suggest that niche segregation rather than competitive exclusion is the predominant outcome resulting from competitive interactions. Although there are few studies that compare the importance of different resource axes in separating species, habitat segregation appears to be the most prevalent resource-partitioning mechanism identified for lake and stream fishes (Grossman et al. 1998). However, most observational studies do not test directly whether competition is the most plausible mechanism responsible for the patterns observed or whether other uncontrolled factors could give rise to similar results. For example, allopatric speciation with posterior contact (Wiley and Mayden 1985) can generate patterns equivalent to the competition hypothesis because of differential adaptation to distinct habitats.

In lake systems, the strongest evidence for competition comes from a combination of observational and experimental studies conducted on centrarchid assemblages that demonstrated that competition caused shifts in habitat use, thereby facilitating exploitation of different food sources (Werner 1984). In a review of the literature involving numerous assemblages, Robinson and Wilson (1994) found that habitat diversification appears to be the mechanism allowing coexistence of lake fishes. In addition, they showed that evolutionary responses to competition, such as character displacement promoting morphological differences, especially between benthic and pelagic forms, are much more common than previously considered. Recognizing that habitat is an important component of the niche for a variety of lake species highlights an important evolutionary consideration. Given that similar habitats occur in lakes in very different parts of the world, it is not surprising that comparable habitat segregation occurs in many areas. Although the species composi-

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tion may be quite different, ecological equivalents are represented in these different regions. This convergence of ecotypes from disparate regions implies that habitat differentiation is very important because habitats are relatively more stable over evolutionary times than other resource parameters such as food quality and availability. In fact, Jackson et al. (1992) suggested that habitat-related differences and predation effects, rather than competition, structure lake fish communities.

In contrast with that for lake fish communities, the knowledge of competitive interactions in structuring stream fish communities remains somewhat superficial (Resetarits 1997). There are several studies showing the presence of competition among stream fishes (e.g., Resetarits 1997). However, due to the environmental variability in stream systems, ecologists continuously debate whether behavioral, morphological, and physiological adaptations play a more important role than interactions such as competition (Grossman et al. 1998). The net increase of species richness along gradients of high to low environmental variability (Gilliam et al. 1993) and the fact that average population densities are often far below the maximum have been used to argue that competition is less important in shaping stream community structure. Populations in variable environments could be stable but at densities below where competition becomes important. Streams simultaneously may have both "harsh conditions" where disturbance might play an important role and "benign environments" where interactions could be significant due to environmental stability (Townsend 1989). There are dissenting views (Lóbon-Cerviá 1996; Rodriguez and Lewis 1997) regarding the importance of spates and droughts as population controls in streams given the associated stress and potential for population decline during such events. Much of the controversy regarding the importance of competitive interactions in structuring stream fish communities may arise from different scales being used in different studies (Taylor et al. 1993). The importance of the range in habitat conditions and spatial scale is critical in whether competition is viewed as an important factor or not.

Most freshwater fish ecologists now accept the idea that combinations of local biotic and abiotic factors with associated regional factors are responsible for structuring local communities (e.g., Angermeier and Winston 1998). However, the accumulation and interpretation of evidence from numerous isolated small-scale studies does not provide a suitable basis for interpreting large-scale patterns (Underwood and Petraitis 1993). We need to determine whether competition can influence community structure at scales that are larger than the "garden experiments" that are commonly used in resource limitation experiments.

Only recently have stream fish ecologists started to interpret evidence of competition from empirical observation or natural experiments over large spatial scales, where other processes that could have led to equivalent patterns are partitioned out in the design and analysis. Winston (1995) presented a compelling case in which null models rather than controlled experiments were used to investigate whether interspecific competition was a more parsimonious explanation for patterns of species co-occurrence relative to other alternative hypotheses such as history (see Douglas and Matthews 1992). Natural experiments not only accommodate larger numbers of species, geographic and time scales, treatment levels, and their combinations, but they can also be used to control for confounding effects that could mimic the results of competition, such as different habitat optimums (e.g., Taylor 1996). Natural experiments have contributed substantially to our insight regarding the importance of competition in structuring stream fish communities, and additional insight can be obtained provided that more adequate sampling and statistical designs and sophisticated analytical tools are applied. Some competitive effects, such as exclusion over large scales, can be best detected through natural experiments. Such resulting patterns can indicate (*i*) at which spatial scales local interactions have an important effect, (*ii*) the resources that appear limiting and therefore under competition, and (*iii*) which species are most likely to be affected, thereby providing the initial evidence for competitive interactions. Where appropriate, additional experiments can help define the specific mechanisms (e.g., density or size compensation, types of resource) through which competition influences population trajectories.

Abiotic factors structuring fish communities

Biotic factors, whether predation or competition, show comparable effects on the fish communities in both lake and stream/river systems. However, the abiotic influences in lakes and streams are quite different in their relative importance in determining the fish community composition. Many of the factors in lakes show variation principally in a vertical orientation whereas stream systems exhibit them in longitudinal arrangements, often semireplicated within pool–riffle pairings along the length of each stream. In general, the abiotic components of both systems can be divided into physical and chemical factors.

Physical

Climatic conditions control the potential range that any given species can occupy. Whether or not species occupy the various sites within this potential range is due to a combination of historic/biogeographic conditions defining the regional species pools (e.g., previous opportunities to colonize the area or in situ speciation) and contemporary factors at a smaller scale (e.g., predation, environmental gradients). This nesting of selective pressures yields the realized set of species at a site, i.e., the community, relative to the regional pool of species defined by the climatic and historical conditions. Smith and Powell (1971) first formalized this relationship such that the local fish community was the product of selection on the global fish fauna by various environmental, biogeographical, and evolutionary factors that were portrayed graphically as a series of screens or filters (Fig. 1). Tonn (1990) presented a similar framework of nested filters removing components of the fauna resulting in the realized local fish community.

Climatic factors can be divided into those related to temperature and those related to precipitation. Temperature has been long recognized to limit the range of species both in a broad geographic scale (e.g., Shuter et al. 1980) and at finer scales within particular lakes or streams (e.g., Grossman and Freeman 1987). High temperatures may produce high physiological demands and stress while also reducing the oxygen

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saturation levels of water. So the combination of increased metabolic demand and decreased oxygen availability can prove limiting or lethal. Aquatic systems may have thermal refugia if they stratify and the hypolimnion remains sufficiently oxygenated (see below). Stream systems often have comparable refugia where deeper pools having groundwater inflows provide refuge from the daily heating during summer periods (e.g., Matthews and Berg 1997).

Low temperatures may limit the distribution of species and affect community composition (Magnuson et al. 1979). Shuter et al. (1980) showed that average July temperatures below 15°C prevented young-of-the-year smallmouth bass from growing to a sufficient size to overwinter successfully, therefore precluding long-term viability of the population. We discussed earlier the impact that this predator has on other species of fish. Therefore, in areas near the northern limits of the range of smallmouth bass, temperature plays a major role in determining the composition of these communities. Winter temperature is important in affecting the mixing regime of lakes and the duration of ice cover for temperate or boreal/alpine lakes. In turn, the mixing regime affects the availability of oxygen in deeper waters of dimictic lakes and the availability of oxygen in monomictic systems, particularly those in warmer climates. Within stream systems, low temperatures can have direct impacts by determining the duration, form, and depth of ice formation. Ice may provide a surface cover, thereby limiting oxygen exchange, or ice may thicken, potentially freezing to the bottom, thereby killing fish directly. Spring thaws can provide severe ice scouring, effectively removing the fish and much of the habitat from the streams (Scrimgeour et al. 1994). Such effects tend to be greater in headwaters of alpine systems or temperate/boreal streams than in the lower reaches. The ability to survive during freezing or scouring conditions differs among species due to behavioral, physiological, and morphological adaptations. Therefore, community composition differs in systems experiencing different levels of the stresses. However, limited research has been directed at studying fish communities during winter months in cold regions. The difficulty in working in adverse conditions has limited our knowledge, and additional work is required given that these periods may represent a substantial proportion of each year and may be the critical periods of the year for some communities.

Lake or stream morphology affects the consequences of local temperature conditions and other abiotic factors (e.g., oxygen). The surface area of lakes is strongly related to species diversity in lakes (e.g., Barbour and Brown 1974). Increased fetch contributes to increased wave action that may lead to the formation and maintenance of coarse, rocky littoral habitats that may not exist in smaller lakes. These habitats may enhance community diversity because these new spawning, nursery, or feeding habitats may not be present in smaller lakes. Area and fetch of lakes influence the temperature of the surface waters, the depth to which mixing occurs, and the associated hypolimnetic volume. The morphology of lakes also influences the proportion of the euphotic or productive zone relative to the hypolimnion. Lakes having proportionately smaller hypolimnetic volumes are more prone to experiencing temperature and oxygen stress, thereby potentially limiting the viability of cold-water species during summer. For a given level of production and respiration, a shallow lake will experience a proportionately greater depletion of oxygen during the winter. Given the taxonomic variation in sensitivity to oxygen stress (see below), morphometric differences among lakes can lead to very different fish communities.

Stream morphology affects flow dynamics, both temporally and spatially. Geomorphology, soil development, and vegetative cover all affect the rates at which precipitation or snowmelt reaches the principal channel. The result is that systems behave very differently depending on the relative contributions of groundwater versus surface flow in combination with the precipitation regime. The degree of variability associated with velocity selects for species capable of surviving within these flow regimes (see Statzner et al. 1988) or those able to recolonize quickly. Some studies show minimal effects on the adults in fish communities even after major floods (e.g., Matthews et al. 1994). The morphology of the streams varies such that some streams have well-developed pool–riffle patterns due to the underlying geology whereas other systems may have geologies that do not readily develop such patterns (e.g., recently glaciated PreCambrian bedrock in north-temperate regions or alpine systems). Morphological features, such as depth, are often strongly related to community composition. Depth of streams is negatively correlated with the probability of winter freezing and oxygen depletion and with high water temperatures during summer periods (Schlosser 1987). Shallow streams are more variable with greater extremes in the range of conditions experienced by the associated communities in much the same way that shallow lakes experience greater extremes annually.

Structural complexity of the environment interacts with other characteristics of the abiotic and biotic environment and contributes to the community diversity. Substrate surface irregularities, such as rocks or woody material (i.e., necromass), alter the stream flow and deepen some regions through hydraulic scouring (Shetter et al. 1946) with fish being attracted to the area because it is energetically less demanding than maintaining a position in the open water. Areas in both streams and lakes with more complex habitat characteristics have been identified as providing both enhanced foraging and enhanced refuge from predation, thereby contributing to increased diversity (Flebbe and Dolloff 1995). In a similar way that hard surfaces enhance diversity, different assemblages may be found depending on the level of macrophyte cover provided, although this is not strictly an abiotic factor.

Chemical

The principal chemical factors affecting community composition identified repeatedly in studies of lake and stream fish communities are dissolved oxygen levels (e.g., Zalewski and Naiman 1984) and the acidity of the system (e.g., Harvey 1975). We indicated the importance of oxygen and its relationship with water temperature (e.g., the capacity of water to hold oxygen decreases as temperature increases while metabolic demand typically increases). In deeper temperate lakes, the fish assemblages become spatially segregated during summer, since species requiring colder, oxygen-rich waters are restricted to deeper waters whereas many of the small-bodied species (e.g., cyprinids) occupy shallow, littoral areas. This reduces some predatory and competitive interac-

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tions within lakes because the species are spatially segregated for a significant portion of the year. In contrast, the principal littoral predators in temperate North American lakes (e.g., bass, pike) occupy similar habitats with these smaller species, and their concentration together in the epilimnion during summers may contribute to patterns of mutual exclusion (Jackson et al. 1992). In shallower lakes, the cold-water assemblages are absent generally due to a combination of both thermal stress and oxygen depletion in the deeper waters. Large predatory species generally require higher levels of oxygen, and many smaller species have behavioral and physiological adaptations that allow them to survive even at low oxygen levels (Magnuson et al. 1985). Therefore, periodic reductions in dissolved oxygen levels contribute to the loss of predatory species such as pike and bass whereas prey species may be relatively unaffected (e.g., Harvey 1981). Small differences in the development of winter anoxia result in very different community composition in adjacent lakes. Streams also exhibit variation in the level of oxygen present, perhaps without the availability of oxygen-rich counterparts (e.g., hypolimnetic waters) being available as a refuge. Shallow, slow-moving sections of streams are prone to temperature elevation and decreased oxygen levels due to high decomposition and respiration rates, thereby stressing fish present or favoring different species. The combination of temperature and oxygen stress may eliminate intolerant species, such as salmonids, from stream systems. Tropical systems having low flow rates, or flood-plain ponds, frequently develop low oxygen levels due to high ambient temperatures and high respiration and decomposition rates. Tropical fishes exhibit a greater degree of air breathing relative to temperate fishes (Kramer 1983), likely reflecting this selective pressure imposed on these communities due to anoxia.

Acidity of lakes and streams has a strong effect on fish communities. Species richness in lakes declines as waters acidify (e.g., Somers and Harvey 1984). Anthropogenic acidification in temperate North America and northern Europe has contributed to the loss of many populations and changes to the fish communities, as many of the small-bodied species are more vulnerable (Rahel and Magnuson 1983) than the larger species, in contrast with the relationship for dissolved oxygen. The potential for acidification is influenced by geology and by the lakes' position within the landscape. Lakes positioned on carbonate-based bedrock and with deeper soils generally show less impact of acidification than lakes located on granitic rocks, assuming that other factors are equal. Therefore, there can be substantial differences in the water chemistry and the associated fish communities among lakes at relatively small scales (e.g., kilometres; Somers and Harvey 1984) as well as differences between regional faunas and communities at larger scales (e.g., tens to hundreds of kilometres; Jackson and Harvey 1989). Location in the watershed also contributes (Kratz et al. 1997) because headwater lakes generally acidify more quickly than downstream lakes as lake surface area represents a greater proportion of the total catchment area; therefore, it provides less potential to buffer the precipitation. These headwater lakes experience a loss in species diversity even though they generally begin with a more depauperate fauna because species richness is correlated with lake size (Magnuson 1976). Some regions contain naturally occurring acid lakes or streams due to the presence of high concentrations of organic acids originating from adjacent wetlands. The fish communities of these areas have undergone long-term selection for such conditions whereas anthropogenic acidification has been mainly restricted to the past two to four decades, generally not providing sufficient time for selection or for colonization by tolerant species.

Scale and spatial aspects of fish communities

The aspects of scale and space are somewhat interrelated given that large-scale studies involve greater spatial areas than small-scale studies or, alternatively, incorporate greater periods of time. Although we consider scale separately from the biotic and abiotic components, such distinctions are rather artificial, since these three sets of factors are generally interrelated and their interactions confound attempts to separate out specific main effects. The perceived importance of various abiotic or biotic factors is generally dependent on the scale at which the study is carried out. Moreover, biotic interactions and population dynamics are clearly related to variation in abiotic components (Power et al. 1988).

Within terrestrial and aquatic systems, one finds that habitat and environmental heterogeneity increases with the spatial or temporal scale (Zalewski and Naiman 1984). Studies examining the relationship between habitat and fishes tend to focus at one of two scales (Hinch 1991). Lake studies either compare in detail the fish assemblages and habitat use at different sites within a lake, often through time, or operate at a larger scale, examining the compositional patterns among lakes using each lake as an observational unit (e.g., Johnson et al. 1977) with less accurate or precise estimates of the abundance of species. Many of the studies at the large scale simply use species presence–absence as the level of data resolution due to the difficulties in obtaining reliable estimates of relative or rank abundance (see Jackson and Harvey 1997). Similarly for stream studies, researchers focus on obtaining detailed data at very small spatial scales or less detailed data for larger comparative studies (Lamouroux et al. 1999). In the case of small-scale studies in lakes or streams, researchers often study aspects related to fine-scale habitat use or habitat partitioning and address questions related to direct interactions between species (e.g., competition). The detailed information required at such fine scales prevents comparable studies from being conducted at larger spatial scales (Hinch 1991), at least without considerable cost. Large-scale studies often focus on the degree to which major environmental conditions (e.g., pH, maximum or minimum temperature, oxygen conditions) are related to community composition and typically find stronger relationships between these patterns than do fine-scale studies. One factor contributing to this scale-related difference in the importance of abiotic factors is the degree of variation found in the sites sampled. Small-scale studies are usually more limited in the range of these environmental variables (e.g., range of *A* to *B* in Fig. 2) whereas the range in the variation is emphasized in the large-scale comparisons. This difference in the range of variation associated with variables makes it difficult to detect significant effects of these environmental conditions. In contrast, the large-scale studies may lack the data resolution to

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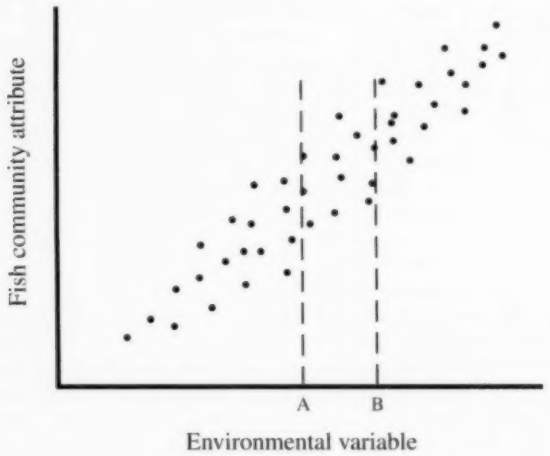
Fig. 2. Importance of the range considered for any environmental variable in whether it shows a strong relationship to a community attribute. We see a strong relationship between the variables if the entire range of the environmental variable is included. However, if we restrict the range of this variable (e.g., *A* to *B*), we lose the ability to detect the significant association. This effect occurs when we choose studies encompassing a large scale with many locations versus the small spatial scale, but intensively studied sites common in studies of biotic interactions. The large-scale studies typically find significant associations with the abiotic factors whereas the small-scale studies do not find the same relationships.



detect effects due to some small-scale environmental conditions and biotic effects such as competition, particularly given that the large-scale studies may not encompass the same species across the sites, thereby preventing direct observations between these species across the sites. So there has been a trade-off in the level of information collected depending on (*i*) whether the researcher's hypothesis is directed towards competitive interactions (e.g., Werner 1984) or major abiotic constraints (e.g., Magnuson et al. 1998) or (*ii*) whether a researcher has the resources to carry out the large-scale versus small-scale studies, which may affect which hypotheses is examined.

Some characteristics of aquatic systems are likely to make spatial scale a more important determinant of community structure than in terrestrial systems. Stream systems incorporate a strong longitudinal pattern given their long length relative to width. There are few, if any, terrestrial ecosystems that show such consistent longitudinal patterns throughout the world. This corridor-like formation leads to many attributes unique to stream systems. Studies at small scales identify differences in the microhabitat available and the types of fish assemblages found therein (Grossman and Freeman 1987). Such differences relate to characteristics associated with substrate, flow, and structure providing cover and often are identified at scales within a few metres that encompass either a pool or a riffle habitat (Cooper et al. 1998). However, increasing the level of spatial scale includes greater differences among the habitats, since pools and riffles may be contrasted within the same study. The differences in substrate, depth, flow, and oxygen are now greater when pool–riffle contrasts are included. Increasing the scale further often does not provide a comparable jump in the range of habitats considered because stream systems incorporate semireplicated patterns of pools–riffles along the length of the stream. However, increasing the scale to include the entire length of the stream or multiple streams often leads to a substantial increase in the range of habitat conditions because there are major differences in environments from headwater to stream mouth locations (e.g., Vannote et al. 1980 and references therein). There may be considerable differences between watersheds where historical or biogeographic factors provide constraints on the communities by defining the regional pool of species from which the species can be drawn (e.g., Matthews and Robinson 1998). At smaller scales, local environmental gradients constrain the set of potential species from the regional pool with biotic interactions (predation, competition), leading to the realized communities at a local scale (Fig. 1). Much of our understanding about the importance of environmental gradients in organizing stream fish communities has been from studies at intermediate and small scales along longitudinal gradients within streams (Rahel and Hubert 1991), along pool–riffle sequences (Angermeier and Schlosser 1991), and in microhabitat use (Grossman et al. 1998). Local-scale factors are usually easier to measure, identify, and correlate with fish distributions than large-scale processes (Lamouroux et al. 1999) but are also more variable temporally. If local processes persist over intermediate (e.g., streams from different watersheds) and large scales (different watersheds), they can contribute dramatically to our understanding of community organization (Levins 1992).

Some important generalizations have arisen about the role of abiotic factors in structuring stream fish communities along longitudinal stream gradients. The main patterns of longitudinal succession of fishes in streams are the addition and substitution of species along gradients (Gilliam et al. 1993). Additions of species are usually related to environmental gradients having relatively smooth transitions of abiotic factors along longitudinal stream profiles (Vannote et al. 1980) and will contribute to more nested patterns of community composition (i.e., sites having fewer species are simply subsets of more speciose sites; e.g., Taylor 1997) whereas species substitutions correspond to abrupt discontinuities in stream geomorphology or abiotic conditions (e.g., temperature), promoting isolation of the site and species (Balon and Stewart 1983). The continual addition of species from small headwater streams to larger rivers is a consistent pattern in most temperate and tropical stream fish communities (Matthews 1986). This pattern is attributed mainly to the increased habitat diversity and stability downstream along watershed gradients (Meffe and Minkley 1987), with these components of the physical environment being positively associated with the variability of stream flow (Statzner et al. 1988). Lower-order streams support low diversity and less-structured assemblages due to a relatively high variability in their environment. Recolonization dynamics, temporal variation in reproductive success, and the ability to find suitable refugia during harsh conditions appear to be more important than biological interactions as determinants of community organization in such streams (e.g., Schlosser and Kallemeyn 2000).

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Physical disturbance reduces the densities of populations with the result that biotic interactions may not appear as important as abiotic conditions in determining community structure (Jackson et al. 1992). Temporal heterogeneity associated with stream habitat characteristics provides an important factor influencing fish communities. The major form of environmental variability (e.g., frequency, magnitude) in stream ecosystems is fluctuation in stream flow. Changes in these characteristics alter the physical habitat of streams and rivers, thereby influencing the composition and stability of fish communities (e.g., Grossman et al. 1998), primarily due to increased mortality and a reduction in recruitment. Response of fish assemblages depends on the degree of change relative to the flow regime and how various geomorphic and ecological processes respond to this relative change (Poff and Ward 1990). Furthermore, longitudinal and lateral variation in stream discharge can lead to complex spatial and temporal dynamics of fish populations and communities (see Schlosser (1991) for examples). In higher-order streams, where the catchment area is larger and thus hydraulic variation is lower, habitat characteristics are more stable and communities are able to persist for relatively longer periods of time. Maximum diversity is likely to occur in sites where the habitat diversity is enhanced and strong interspecific interactions are mediated by intermediate environmental disturbance (Resh et al. 1988). Zalewski and Naiman (1984) proposed a conceptual model where there is a gradual shift from abiotic to biotic regulation of stream fish communities as stream order increases.

Research on associations between environmental characteristics and the distribution and abundance of fish species across space has contributed greatly to our understanding of the relative importance of local abiotic and biotic factors (or combinations of them) in determining community structure (e.g., Taylor et al. 1993), whether species–environment relationships persist over intermediate and large spatial scales (e.g., Lohr and Fausch 1997), and whether environmental variables remain associated with fish assemblages at different levels of spatial scales (low- versus high-order streams, riffles versus pools; e.g., Grossman et al. 1998).

Although we have focused on stream systems in examining the role of scale and the interplay between abiotic and biotic components, similar results are found from studies of lake fish communities. Small-scale studies incorporate more limited contrasts of environmental conditions and tend to emphasize the importance of competitive interactions and habitat partitioning (e.g., Werner 1984). In very small lakes, there is a much greater temporal variation in environmental conditions (i.e., greater variability in temperature and oxygen), but less spatial variation, than in larger lakes. This increased variability likely contributes to annual or periodic reductions in species abundances due to thermal or oxygen stress, thereby reducing the potential for competitive interactions because resources may not become limiting (Jackson et al. 1992). With larger lakes, the environmental variability is dampened through thermal inertia, and stratification provides cold-water habitat throughout the year. Larger lakes also have greater habitat diversity and generally greater species richness (Magnuson 1976). This parallels the species addition effect found in streams. Studies incorporating multiple lakes tend to include lakes differing in size, thereby having systems exhibiting different degrees of environmental variability. This range in variability over time and space emphasizes the importance of abiotic factors in structuring lake communities at large scales, in contrast with small-scale comparisons emphasizing competitive interactions (Fig. 2). In contrast with competition being most evident in small-scale studies, both large- and small-scale studies identify predation effects, thereby indicating its importance in structuring fish communities within and across scales.

Spatial dynamics

Although the role of space in habitat heterogeneity is widely recognized, the importance attributed to spatial aspects in population and community dynamics has increased recently (Hanski 1999 and references therein). Many of these terrestrial and theoretical studies show the importance of spatially structured populations (e.g., metapopulations) in the maintenance of species diversity and community composition. The movement of individuals between habitats can reduce the rates of local extinction as well as permit recolonization following local extinctions. The rates of interpatch movement have important implications ranging from population genetics to community composition. To date, there has been limited recognition of the role of spatial isolation and metapopulation dynamics within aquatic systems. Some early studies identified the similarity of lakes (Barbour and Brown 1974) and rivers (Eadie et al. 1986) to islands or insular habitats. A few studies have attempted to quantify the degree to which lakes are isolated from one another (e.g., Magnuson et al. 1998) based on measures of the connections between lakes. The degree of habitat insularity in streams and lakes depends on a number of natural and anthropogenic conditions. Seepage lakes show complete isolation from other aquatic habitats (Magnuson 1976), except during periods of extreme flooding or human stocking activities. Isolation among drainage lakes is a function of the number, length, and suitability of connecting watercourses (Olden et al. 2001). Suitability of a watercourse for fish movement depends on the number and magnitude of artificial (e.g., water regulation dams) and natural barriers (e.g., beaver dams, waterfalls), stream morphology such as the number of stream confluences, the prevalence of seasonal drying or warming of streams, and channel characteristics such as depth. Within-stream connectivity is determined by these systems factors, but the role of beaver dams has been identified as providing a temporally varying barrier or facilitator to dispersal, both because the dams have limited life spans and because different species may benefit from the creation of standing water habitat (Snodgrass and Meffe 1998). Beaver dams and ponds are direct barriers to upstream dispersal and may provide unsuitable habitat because other species (e.g., predators) may predominate in the ponds, or alternatively, the ponds serving as "stepping stones" aid in the dispersal of species throughout a stream system. Piscivory influences the degree of isolation among habitats by imposing a risk of predation on potential dispersers. Increased density of piscivores may have conflicting effects in reducing the rate of movement by killing and (or) blocking prey as well as increasing movement by inducing prey to disperse from side pools or climb cascades to escape predators (see Gilliam and Fraser 2001).

Despite the fact that aquatic systems seem to be ideal models of habitat patches and connecting corridors, there is

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limited evidence indicating whether fish communities show metapopulation characteristics (e.g., Gotelli and Taylor 1999), and few studies document limited rates of movement of species. Hill and Grossman (1987) showed that stream fish movements were small, on the order of metres, over extended periods of time. This contrasts with other findings (D.A. Jackson, unpublished data) showing high rates of movements of some species between lakes (25% of recaptured white sucker (*Catostomus commersoni*) and 5% of smallmouth bass were recaptured in lakes other than where they were tagged). Given the frequency with which some shallow lakes experience lethal environmental conditions during the winter or summer, it is likely that recolonization is an essential factor in the maintenance of lake fish communities. Fish species differ in their abilities to move through these connecting waterways. Different streams vary in their characteristics, either facilitating or preventing the movements of various species (providing selective filters based on the temperature and flow characteristics of the streams). The interaction of the species and stream characteristics contributes to differences between communities, even in lakes with similar environmental conditions. Increased rates of transfer of particular species (i.e., sport fishes) between water bodies due to human activities are leading to more consistent or homogenized fish communities (Rahel 2000). Given the noted effects that many of these introduced species have as dominant littoral predators, their strong impacts on the indigenous fish community contribute to a loss of biodiversity, particularly among-lake diversity.

Spatial dynamics and habitat heterogeneity are also of concern in the maintenance of biodiversity within lakes frequented by humans. Many lakes undergoing development by humans actually have reduced habitat heterogeneity, thereby reducing the potential for habitat segregation and refuge from predation. Cottagers modify existing habitats by removing macrophytes and woody structures in favor of sandy beaches or shore with retaining walls. The net effect is the opposite of habitat fragmentation in that many of these lakes are actually experiencing habitat homogenization as the lakes become increasingly developed and lacking in spatial complexity.

Advances and challenges in fish community ecology

This section identifies problems that seem to be limiting our current understanding of fish community ecology and highlights those promising areas of research or areas that we believe represent priorities for future research. We chose such areas due to either technological advances or theoretical and empirical advances from other fields (e.g., terrestrial ecology) that indicate areas of promise or, alternatively, because of the potential implications of ignoring areas.

The spatial dynamics of populations and communities are an important topic that is being virtually ignored within the context of aquatic systems, in particular by resource managers. Although terrestrial and theoretical ecologists have carried out extensive work related to spatial dynamics of single species or communities (see Hanski 1999), there is limited work examining lakes (e.g., Olden et al. 2001) and streams (Schlosser and Kallemeyn 2000). Whether this reflects a general lack of interest or the associated costs of monitoring movements of fishes in aquatic systems is uncertain. Having this information would help integrate the roles of biotic and abiotic factors across varying spatial scales by determining more precisely how individual fish are using space to minimize biotic and abiotic stress. Human activities are modifying habitats in stream systems and groups of lakes to varying degrees. Changes in the connectivity due to damming or alterations to flow patterns, coupled with habitat modification, may threaten the long-term viability of existing populations and communities. We have a severely limited knowledge base from which to predict outcomes or identify risk. Spatial dynamics are important for understanding the basic ecology but also need to be recognized by resource managers. For example, typically the management of a lake sport fish population is carried out without considering that populations in nearby lakes may be directly linked and that management decisions (e.g., stocking of bass) may have direct implications for the communities in the nearby lakes. Planning for stocking programs generally assumes that there is limited, if any, exchange of individuals between systems. This current paradigm of viewing lakes and streams is outdated. It fosters mismanagement of the resources and fails to recognize the mechanisms by which introduced pathogens and exotics can quickly impact an entire regional fauna. In contrast with this "isolation" paradigm, restoration projects often assume implicitly that such movements between water bodies will occur and provide the seeds for a recovery of the community, but we do not know how realistic such assumptions may be. We need an information base about the degree of fish movement within and between lakes and streams to better understand the mechanisms necessary for the maintenance of fish communities.

The application of advancing technologies, such as radiotelemetry and stable isotope methods, is promising. Telemetry methods provide a better definition of a species' spatial occupancy and the movements of individuals and their use of particular habitats. Telemetry can provide insight into the linkages between specific habitat features and the members of a fish community, particularly given that the use of such features may vary depending on time (day versus night or seasonally) and due to ontogenetic changes in the fishes. To date, much of our knowledge has been gained by netting or trapping of fish that integrates long periods of time. The dynamic nature of individuals and their interactions with other species is lost in such coarse levels of detail. In contrast, the real-time information obtained from telemetry approaches can provide a wealth of information about community dynamics not available previously. Determining the relative importance and timing of use of various habitat types both provides a fundamental understanding of the use these features by the various community constituents and provides managers with an improved array of methods to minimize potential impacts during development or resource exploitation. Such technology provides the basis to determine detailed information about physiological processes, small-scale environmental conditions, and larger-scale use of lakes or streams over time. Stable isotope and hard tissue chemical analysis can provide information related to the individual dates of movements between freshwater and saltwater systems, alterations to energy flow as a result of changes to adjacent

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terrestrial habitats, and historical measures of ecosystem impacts due to species introductions (e.g., Vander Zanden et al. 1999). Such techniques provide sophisticated approaches to recreate historical conditions and timing of events, similar to the goals of paleolimnologists.

Another area where additional effort would be particularly valuable is extended temporal data sets. The limited nature of long-term monitoring of fish communities in lakes and streams (e.g., Long Term Ecological Research Areas (LTER)) is highly constraining. The number of sites involved and the range of communities and environmental conditions currently studied are very limited. This scarcity of long-term data sets necessitates that spatial comparisons be used to study the mechanisms regulating communities whereas temporal comparisons may provide better information for specific hypotheses. The "space-for-time" substitution is often used but may not be appropriate in some or perhaps many cases. Currently, we do not know whether the substitution is appropriate. It is these long-term programs, employing consistent sampling approaches, that provide us with an understanding of the temporal dynamics of fish communities. These studies can provide estimates on natural rates of colonization and extinction and direct linkages connecting changes in habitat and responses by species and communities. Such temporal information is critical (Lester et al. 1996) in detecting the impacts of large-scale environmental changes (e.g., acidification, climate change) as well as providing our basic ecological understanding of fish community regulation. Currently, there is considerable concern related to potential changes in abiotic conditions within streams and lakes due to climatic warming. Given that species generally have limited rates of dispersal between watersheds (unless moved by humans), major shifts in environmental conditions will likely prove adverse for fish communities, given the lack of time to compensate or disperse. However, despite these concerns, given our lack of current LTER programs, we will likely not be in a position to determine if such changes do occur unless additional programs are established and their data made widely available.

We need to develop new approaches to assess the relative importance of environmental conditions and species interactions in the structuring of fish communities. Although the organization of fish communities has been credited to a balance between abiotic factors and biotic interactions, studies usually emphasize one over the other. It is important to note that both components are not only complementary and interactive, but their effects can have similar roles in organizing communities, thereby complicating our advancement in understanding community processes. Therefore, studies including different components and using both experimental and observational approaches are necessary to disentangle biotic and abiotic effects and measure their relative magnitudes. Experimental studies usually emphasize the importance of interactions with or species-specific responses to particular abiotic variables (e.g., swimming speed) whereas field studies frequently establish the importance of abiotic variables by establishing correlations between species distribution and environmental gradients. Differences in methodological approaches to studying the roles of biotic versus abiotic structuring have limited our understanding of various issues, such as the role of disturbance in organizing fish communities and whether species that are environmental generalists are more or less sensitive to biotic interactions. Unless we develop studies to determine whether findings from a fine scale hold at larger scales (e.g., Angermeier and Winston 1998), we will be hampered in our abilities to understand the regulation of fish communities. Therefore, there is a great need for studies employing such multiscale approaches that incorporate both experimental and correlative approaches.

Fish community ecologists have not capitalized on many advances in analytical approaches from other fields (e.g., engineering, medicine). We have a large body of literature related to various fish species and whole communities and their association with various biotic and abiotic factors. However, we appear to be ignoring the opportunities that these present, and there has been little attempt to capitalize on this information base. The use of meta-analysis (e.g., see Englund et al. (1999) for a recent application) could serve to help partition out some of the factors summarized in our paper. The ability to separate the effects of various factors and their strengths has the potential to partition the relative roles of biotic, abiotic, and spatial components in shaping fish communities. With the extensive information at hand, a means of evaluating our understanding and predictive power is to determine the degree to which we can correctly identify the various members of communities based on the associated environmental conditions. Being able to correctly identify the communities at a series of sites provides an excellent test of our understanding, provided such tests are implemented correctly (e.g., using appropriate methods to test and validate our models; see Olden and Jackson 2000). Although some studies have developed predictive models based on single species or assemblage types (e.g., Magnuson et al. 1998), we should be trying to develop models that can predict whole communities. Such tests of the entire membership of communities will provide a measure of the state of our knowledge and identify where we are lacking. Advanced analytical tools commonly found in other disciplines, such as artificial neural networks, genetic algorithms, and classification trees, and various multivariate approaches provide the opportunity to test our hypotheses regarding the structuring of communities and provide predictive models. In many cases, one can make strong arguments for improved and more detailed analysis of existing data to address questions, but it is often easier to convince funding agencies of the need for additional data collection rather than more extensive examination of information in hand.

Clearly, there has been no common consensus in the literature regarding the importance of various factors in determining the communities of species associated with various sites. The scale of the study interacts with the biotic and abiotic variables such that the relative importance of biotic and abiotic factors changes across spatial scales. Small streams and lakes are more variable in their abiotic environments than are larger ones. The associated extremes in the environments may affect the larger species, frequently predators, to a greater degree than the small-bodied species, often leading to their local extinction. The loss of these predatory species then contributes to a more diverse community of small-bodied species. The degree to which environmental disturbance keeps the abundances of these species well below carrying capaci-

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ties likely determines whether competition becomes important in structuring the communities. Obviously, we present a generalization, as many exceptions exist to this conceptual model, and similarly, we provide a selectively limited review of the state of knowledge. We have set out to identify the progress made over the past century in understanding the factors regulating fish communities, and we hope that our paper will stimulate discussion and new ideas and contribute to formal model development in both theoretical and statistical contexts.

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Effects of the Hudson Strait outflow on the biology of the Labrador Shelf[1]

K.F. Drinkwater and G.C. Harding

Abstract: Physical, chemical, and biological data collected on the Labrador Shelf in September 1985 are used to examine a hypothesis that the nutrient influx from Hudson Strait increases primary production on the northern shelf and this supports a "conveyor belt" food chain as the community is transported southward by the mean circulation. This hypothesized influx of production was proposed to account for the higher fish abundance on the southern Labrador Shelf. If true, the hypothesis suggests that the relative importance of higher trophic levels generally should increase southeastward along the shelf. Our results confirm that high nutrient levels occur on the northern Labrador Shelf in summer because of continuous advection of nutrients from Hudson Strait and this enhances local plankton production. However, nutrient, chlorophyll *a*, plankton species, and biomass spectra distributions generally do not support the idea that a developing food chain is advected progressively southward along the shelf. The large fish population on the southern Labrador Shelf appears to have been more dependent on production supported by local upwelling around Hamilton Bank than on food advected from the north.

Résumé : Des données physiques, chimiques et biologiques relevées sur la plate-forme du Labrador en septembre 1985 ont permis d'évaluer l'hypothèse selon laquelle l'influx de nutriments par le détroit de Hudson augmente la production primaire sur la plate-forme nord et qu'il entretient une chaîne alimentaire de type « courroie de transmission » à mesure que la communauté dérive vers le sud, emportée par la circulation moyenne. Cet apport de production a été suggéré pour expliquer l'abondance plus grande de poissons sur la partie sud de la plate-forme du Labrador. Si l'hypothèse est exacte, l'importance relative des niveaux trophiques supérieurs sur la plate-forme devrait augmenter vers le sud. Nos résultats confirment l'existence de fortes concentrations de nutriments sur la partie nord de la plate-forme du Labrador en été à cause de l'advection continuelle de matières nutritives depuis le détroit de Hudson, ce qui favorise la production locale de plancton. Cependant, les données sur les nutriments, la chlorophylle-*a*, la composition spécifique du plancton et les spectres de distribution de la biomasse n'appuient pas l'hypothèse qu'une chaîne alimentaire se développe progressivement par advection vers le sud de la plate-forme. Le fort peuplement de poissons sur la partie sud de la plate-forme du Labrador semble donc dépendre plus de la résurgence locale autour du banc de Hamilton que d'un apport de nourriture arrivant du nord.

[Traduit par la Rédaction]

Introduction

It has long been recognized that the temperature and salinity characteristics of the waters over the Labrador Shelf originate in Hudson Strait (Iselin 1927; Dunbar 1951; Kollmeyer et al. 1967). They form from a mixture of cold Baffin Land Current waters flowing southward along the Baffin Island Shelf, relatively warm deep waters that are of West Greenland Current origin, and low-salinity waters flowing eastward from Hudson Bay and Foxe Basin (Smith et al. 1937; Sutcliffe et al. 1983). These water masses converge at the eastern entrance of Hudson Strait, where strong tidal currents lead to intense vertical mixing (Griffiths et al. 1981; Drinkwater and Jones 1987). The residual current carries this resultant mixture onto the Labrador Shelf. The intense mixing causes a reduced range in temperature, salinity, and stratification on the northern Labrador Shelf relative to the Baffin Island Shelf north of Hudson Strait (Lazier 1982; Sutcliffe et al. 1983). The mixing also elevates the surface nutrient concentrations within Hudson Strait (Drinkwater and Jones 1987) and subsequently on the northern Labrador Shelf (Kollmeyer et al. 1967; Sutcliffe et al. 1983).

Sutcliffe et al. (1983) observed that fish abundance increased southward along the Labrador Shelf and also found annual cod recruitment to be significantly correlated with salinity fluctuations such that better recruitment was associated with higher salinity. They proposed several hypotheses to explain these observations. The first hypothesis was that the outflow of mixed waters from Hudson Strait results in surface nutrient enrichment and subsequent increased primary production on the northern Labrador Shelf in summer and autumn. Second, this enrichment supports a food chain that is advected southeastward along the Labrador Shelf by the residual currents as it develops. As a consequence of this advection, the higher levels of the food chain (i.e., larger zooplankton and fish) should be found progressively southward. Third, the year-to-year fluctuations in recruitment of Atlantic cod (*Gadus morhua*) arise from variations in the

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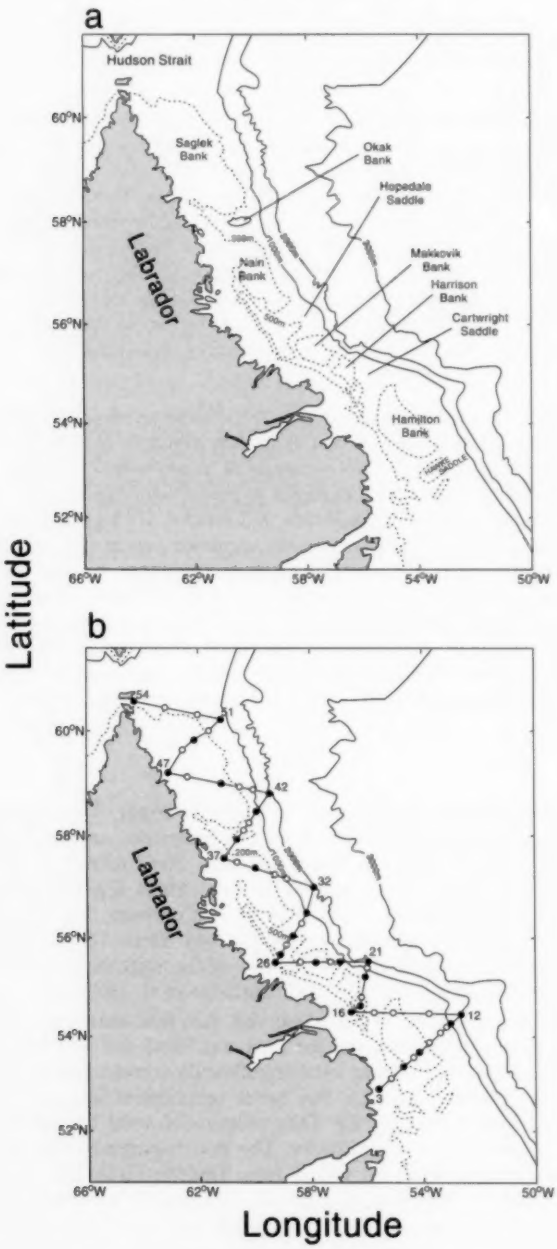

Fig. 1. Labrador Shelf showing (*a*) topographic features and (*b*) the station locations occupied during September 1985. Hydrographic and nutrient data were taken at all stations, while Coulter-Counter® measurements and plankton-net hauls were obtained at those stations marked by a solid circle.

amount of food brought about by changes in the northern nutrient supply, which itself is positively correlated with salinity. Fourth, in years of high freshwater runoff into Hudson Bay, the decrease in salinity results in an increase in stratification. This inhibits mixing at the eastern entrance of Hudson Strait, thereby lowering nutrient levels and salinities on the Labrador Shelf. In support of the latter hypothesis, they noted that the seasonal salinity pattern on the Grand Banks matches that of the seasonal runoff pattern into Hudson Bay after accounting for the estimated time to advect the low-salinity waters from Hudson Bay to the Grand Banks.

Myers et al. (1990) and Petrie et al. (1991) investigated the seasonal salinity cycle on the Grand Banks in greater detail. They found that the late summer – early autumn salinity minimum reflected the arrival of ice melt from the Labrador Shelf rather than the influence of the freshwater runoff in spring from Hudson Bay. Through correlation analysis, Myers et al. (1990) also showed that the effect of the peak river discharge from Hudson Bay reaches the Grand Banks the following spring, not in the autumn as supposed by Sutcliffe et al. (1983). This later arrival time at the Grand Banks was further supported by observations from moored instruments that showed that the lowest salinities in Hudson Strait occurred in late autumn (Myers et al. 1990). These results suggest that the fourth hypothesis of Sutcliffe et al. (1983) is incorrect, i.e., freshwater runoff into Hudson Bay does not play an important role in regulating nutrient supply to the Labrador Shelf in the highly productive summer and early autumn seasons. However, this did not refute the possibility that nutrients mixed into the surface waters of Hudson Strait may initiate a food chain that is advected south as it develops, thereby playing an important role in determining recruitment success in cod to the south. Myers et al. (1993) reexamined the salinity–recruitment relationship of Sutcliffe et al. (1983) using additional runoff and cod recruitment data. They found that it continued to hold through to the early 1990s, just prior to the moratorium on cod fishing, which was imposed after the collapse of the northern cod stock. However, Hutchings and Myers (1994) subsequently found little statistical evidence for the relationship when revised estimates of cod recruitment were used. This puts the third hypothesis of Sutcliffe et al. (1983) into question.

In this paper, we reexamine the first two hypotheses of Sutcliffe et al. (1983). Is there evidence of enhanced primary production on the northern Labrador Shelf that is linked to the outflow from Hudson Strait and, if so, does it initiate a food chain that is advected southward? If the latter hypothesis is correct, the relative importance of the biomass of larger-sized pelagic organisms should increase progressively downstream from Hudson Strait. To test these hypotheses, an oceanographic field study was undertaken in September 1985 when, in addition to physical and chemical observations, we measured biomass size spectra ranging from nanoplankton to small fish over the entire Labrador Shelf region. To the best of our knowledge, our study is the first to use observed pelagic biomass size spectra over many trophic levels to test an advective hypothesis.

Materials and methods

Study area

The Labrador Shelf consists of several offshore banks separated by a series of channels and gullies, known as "saddles" (Fig. 1*a*). In the southern half of the shelf, these banks are also separated from the coast by deep (>500 m) marginal troughs. The largest banks, from north to south, include Saglek, Nain, Makkovik, Harrison, and Hamilton (Fig. 1*a*). The tops of these banks typically lie between 100 and 200 m below the sea surface. Cartwright Saddle

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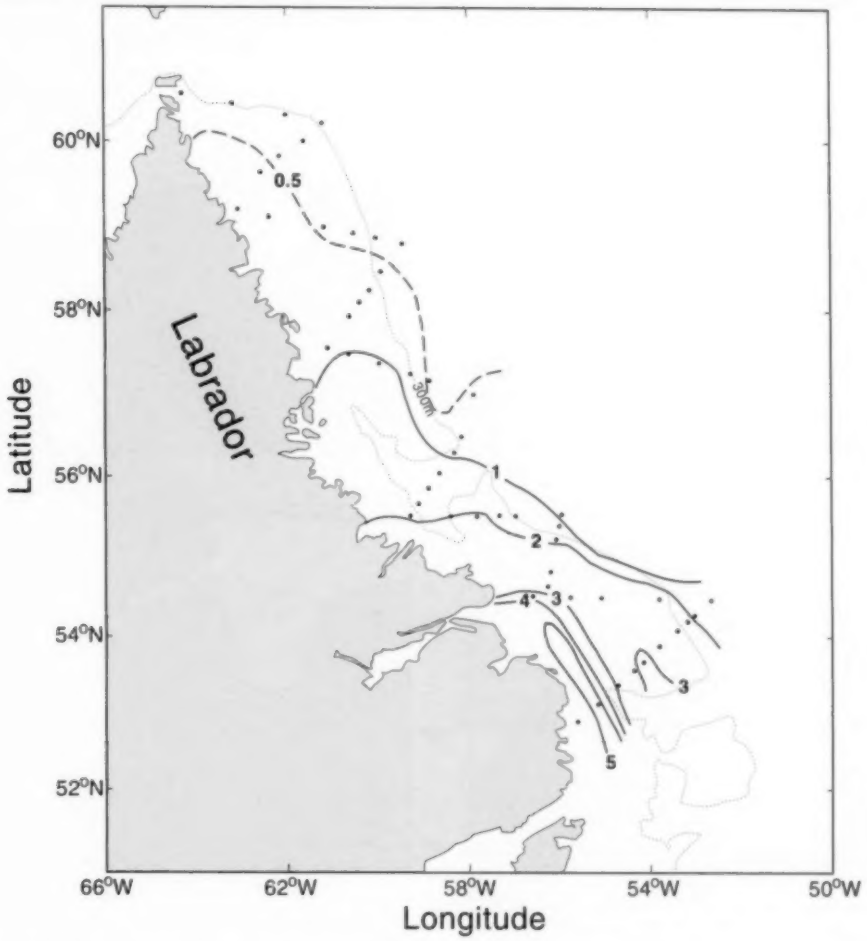
Fig. 2. Sigma-*t* difference (kg·m^{-3}) between 50 m and the surface.



separates Hamilton Bank from Harrison Bank, and Hopedale Saddle separates Makkovik Bank from Nain Bank.

The southward flowing Labrador Current dominates the circulation pattern. The main branch is concentrated over the steep continental slope with surface speeds of 0.3–0.4 m·s^{-1} and an estimated transport by Lazier and Wright (1993) of 4 Sverdrups (Sv) (1 Sv = 10^6 m^3·s^{-1}). The inshore Labrador Current (surface currents of 0.15–0.25 m·s^{-1}, transport of 0.8 Sv) flows along the inner half of the shelf. These two branches of the Labrador Current are separated by generally weak and directionally variable flows over the outer banks (Fissel and Lemon 1991). At times, deep Labrador Sea water flows across the saddles onto the shelf.

Sampling

A total of 10 cross-shelf transects were occupied consisting of 52 hydrographic stations (Fig. 1*b*). At each station, temperature and salinity were measured using a Guildline® CTD (conductivity–temperature–depth) profiler. Salinities are presented in practical salinity units (psu). Salinity calibration samples were collected at a minimum of three depths from bottles on a rosette attached to the CTD. Temperature calibrations were obtained from reversing thermometers at these same depths. The bottles on the rosette were also used to obtain nutrient, chlorophyll *a*, and plankton samples at as many as 10 depths. Triplicate nutrient (nitrate, phosphate, and silicate) samples were taken and measured during the cruise using an Auto Analyzer® II. Chlorophyll *a* samples were filtered through 0.45-µm Millipore® filters, dissolved in acetone solution, and run through a Turner® fluorometer. At 26 of the stations (indicated in Fig. 2), the abundance of small-sized particles (1–125 µm), predominantly phytoplankton and protists, was determined with a Coulter-Counter® (50- and 280-µm tubes) from water bottle samples obtained with the rosette. Estimates were obtained for eight separate size categories (1, 2, 4, 8, 16, 32, 64, and 125 µm). Phytoplankton (>25 µm), zooplankton, and nekton were collected from vertical (23- and 73-µm mesh size) and oblique (236- and 456-µm mesh size) net hauls and Vass–Tucker trawls (1600 µm). Nets were opened at ~5 m from the bottom or at 300 m over deep water and hauled to the surface. Plankton collections were size fractionated on a shaking sieve apparatus (Harding et al. 1997) and frozen to –20°C. The plankton species were later identified and the sample wet and dry weight determined. The biomass was estimated for each of 10 different size categories, from 32 µm to 16 mm (32, 64, 125, 250, 509, and 1028 µm and 2, 4, 8, and 16 mm). The Coulter-Counter® and net data were combined to produce the biomass size spectra from 1 µm to 16 mm for each of the 26 stations where net samples were collected. The wet weight of biomass collected on the 25- and 64-µm sieves and the Coulter-counted 16-µm size comprised the microplankton category, the 125-, 250-, and 509-µm sieves the mesozooplankton category, the 1028- and 2000-µm

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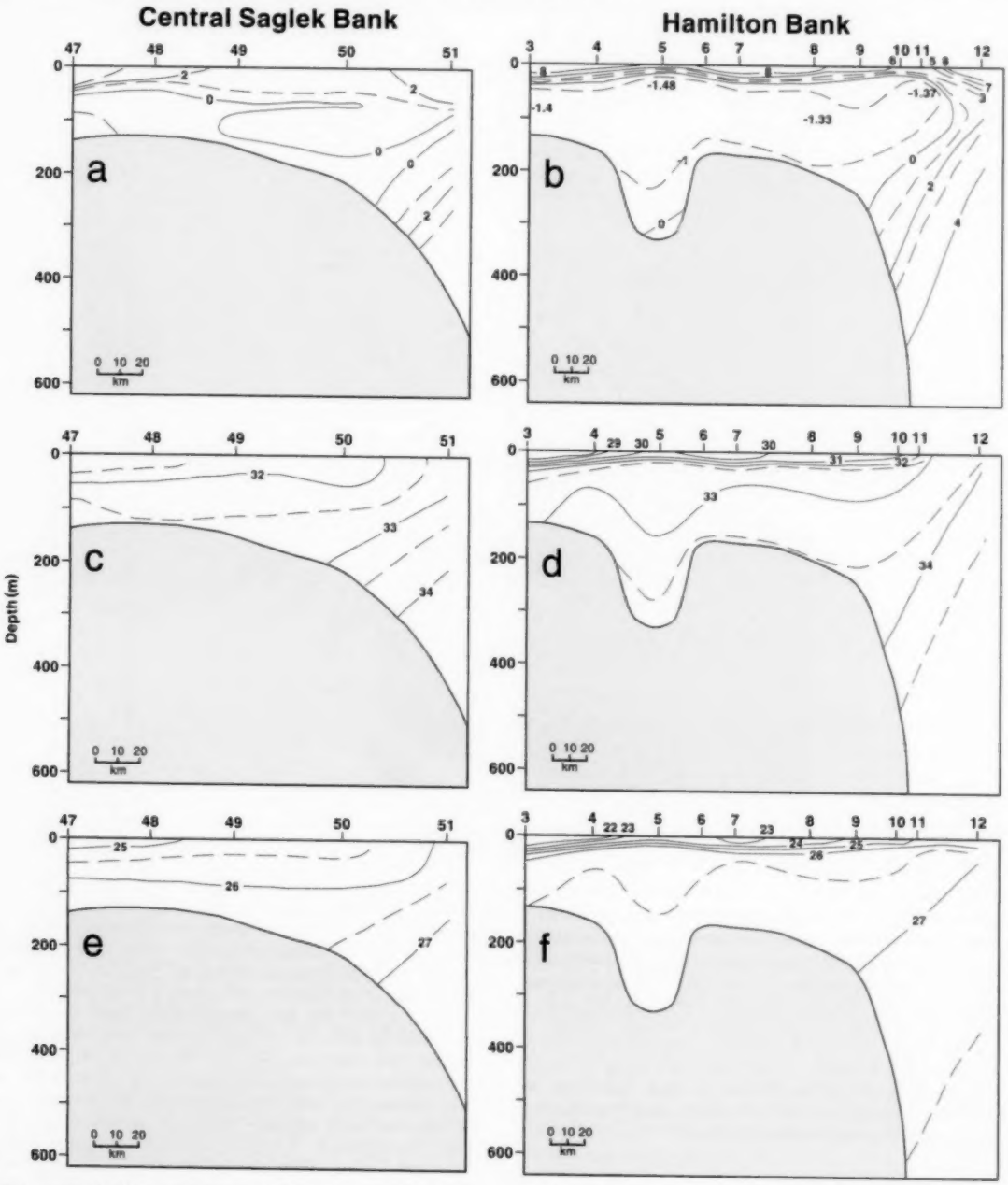
Fig. 3. Contours of (*a* and *b*) temperature, (*c* and *d*) salinity, and (*e* and *f*) sigma-*t* across the central Saglek Bank and Hamilton Bank transects. The station locations and numbers are shown at the top of the panels.



sieves the macroplankton category, and the 4-, 8-, and 16-mm sieves the nekton category.

Data analysis

The spatial variability in the biomass size spectrum was investigated using empirical orthogonal function (EOF) analysis following the method of Sellers (1968). This technique efficiently describes the coherent variability among a number of data sets (in our case, 26 size spectra) by reducing the data set into a smaller number of spectra patterns called "modes." The biomass spectrum (P_i) of sizes s for station i can be rewritten in terms of the sum of the modes (M_j) such that $P_i(s) = \Sigma x_{ij} M_j(s)$, where x_{ij} is the coefficient linking the spectra from station i to the jth mode. The first mode (M_1) accounts for the largest percentage of the variance in the biomass spectra and the second mode (M_2) accounts for the largest amount of the remaining variance. This procedure is repeated for additional modes (M_3, M_4, etc.) until all of the variance is accounted for. Successive modes account for smaller and smaller proportions of the variance. Typically, 80–90% of the variance is

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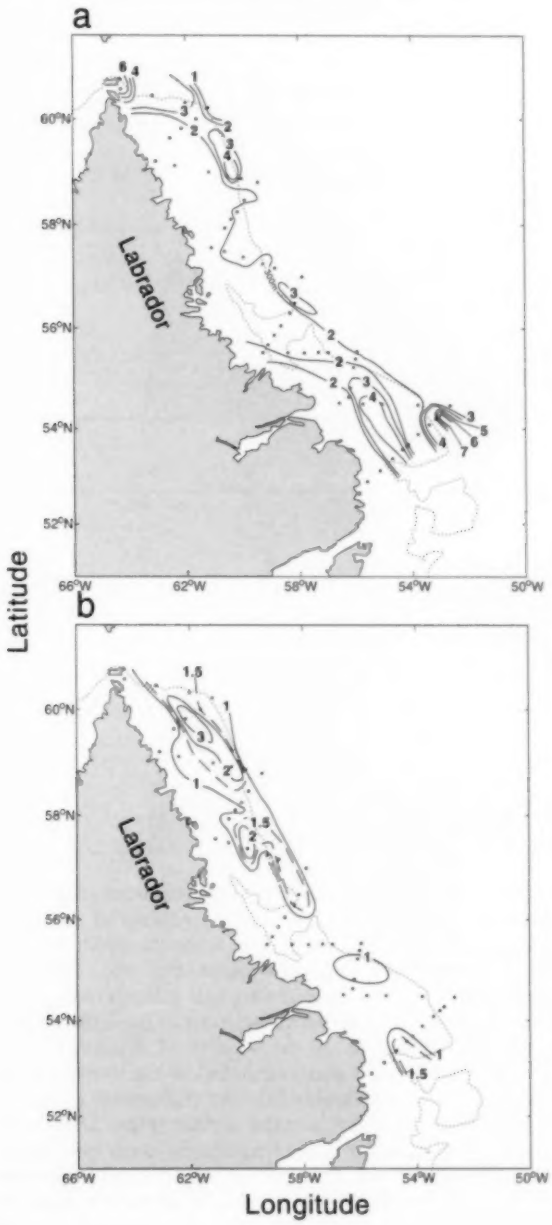
Fig. 4. Contours of the depth-averaged concentration over the top 50 m of (*a*) nitrates (μM) and (*b*) chlorophyll *a* (μg·L^{-1}).



captured in the first two or three modes and the higher modes are not statistically significant. The modes are orthogonal, i.e., the correlation between modes is zero. The coefficients (x_{ij}) are called "eigenvectors" and provide spatial information on the amplitude of the modes.

We defined a stratification index as the difference in water density between 50 m and the near surface. The 50-m depth lies below the surface mixed layer in all stations but two. Nutrients and chlorophyll *a* were depth integrated over the upper 50 m assuming linear interpolation. Depth integration over the surface mixed layer was also carried out for comparative purposes.

Results

Temperature, salinity, and stratification

Water column stratification over the Labrador Shelf during our study generally increased towards the south and inshore (Fig. 2). The most homogeneous station (54) was adjacent to Hudson Strait with a density difference of only 0.13 kg·m^{-3} over a depth of 260 m. Saglek Bank, in the north, was characterized by weak stratification (sigma-*t* difference over the top 50 m of ~0.5 kg·m^{-3}), low surface temperatures (1–3°C), little to no deep water less than –1°C, and a relatively narrow salinity range (31–33) across the shelf (Fig. 3). In contrast, across Hamilton Bank, the southernmost transect, there was an intense pycnocline at 20–40 m depth, surface temperatures were higher (5–9°C), most of the cross-sectional area below the pycnocline was occupied by waters less than –1°C, and there was a large salinity range (28–34) across the shelf (Fig. 3). Temperatures in the upper 50 m generally increased southward from Cape Chidley to Hamilton Bank, whereas below 100 m, temperatures increased northward, a result consistent with the findings of both Lazier (1982) and Colbourne and Mertz (1998). The prominent salinity gradient was across-shelf with fresher water inshore (Fig. 3). The lowest-salinity waters (<30) were observed in the southern inshore areas and account for the strong, near-surface stratification there. The source of this low-salinity water is the freshwater runoff that flows out through Hamilton Inlet.

Nutrients

Nitrates are generally considered to be the limiting nutrient for primary production during the summer in northern waters (Grainger 1975; Harrison et al. 1982; Welch 1990). High nitrate levels, depth integrated over the top 50 m, were observed near Hudson Strait and appear to spread from there to the outer edge of Saglek Bank (Fig. 4*a*). Other nitrate maxima were found along the continental slope off southeastern Nain and Hamilton banks and over the marginal trough inshore of and extending over Hamilton Bank. These are believed to be a result of local upwelling. Nutrient distributions depth integrated only over the surface mixed layer (to the top of pycnocline, not shown) reveal similar high values on the northern Labrador Shelf that appear to emanate from Hudson Strait. Elsewhere over the shelf, these surface mixed layer nitrate levels were low (typically <0.1 μM), suggesting that the primary producers had depleted the available nutrients. Along the slope and on the inshore edge of Hamilton Bank, nitrates are relatively high immediately below the shallow mixed layer (Fig. 5*b*), which accounts for their maxima when depth integrated over the top 50 m. The shallowing of the isopycnals in these areas suggests active upwelling (Fig. 3*f*).

The vertical nitrate distributions on the northern and southern Labrador Shelf are shown in Figs. 5*a* and 5*b*. In the north, over Saglek Bank, near-surface nitrate concentrations were relatively high (>1 μM) with a weak nutricline (Fig. 5*a*). In contrast, surface layer nitrate concentrations over Hamilton Bank were near zero with a strong nutricline near 50 m at the base of the pycnocline (Fig. 5*b*). Nitrate levels below

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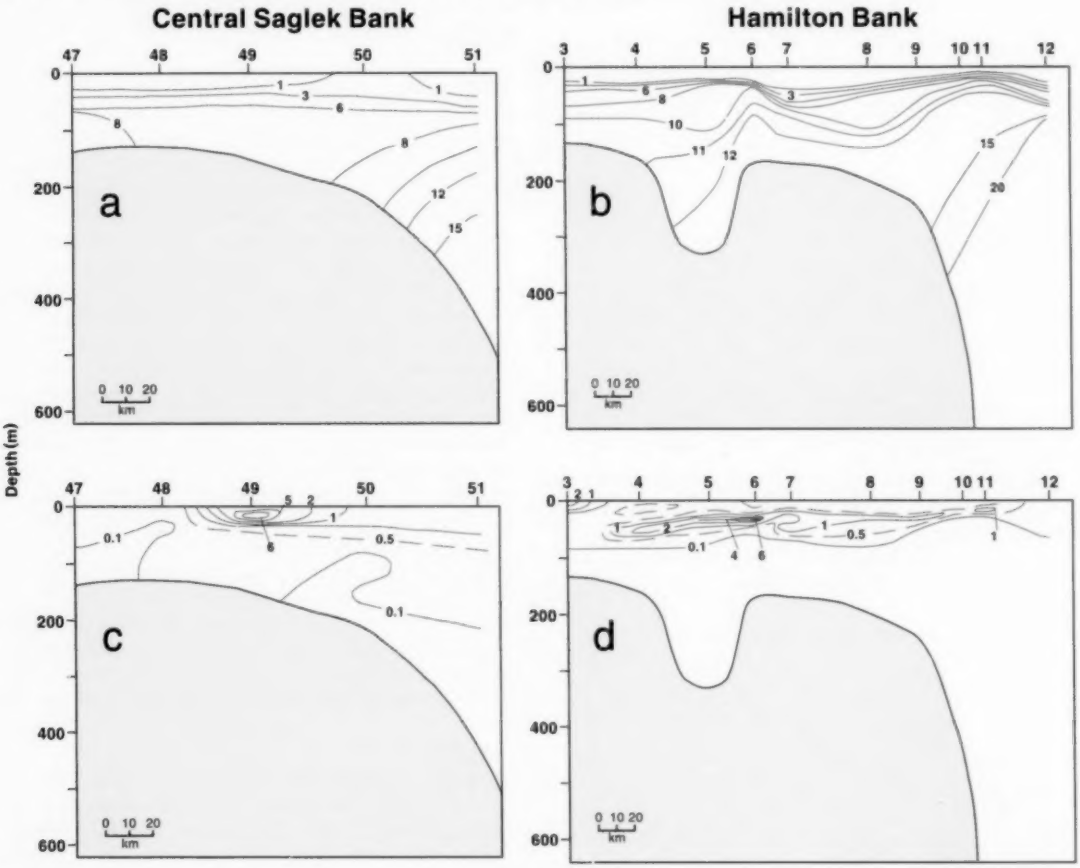
Fig. 5. Contours of (*a* and *b*) nitrate (μM) and (*c* and *d*) chlorophyll *a* (μg·L^{-1}) across the central Saglek Bank and Hamilton Bank transects. The station locations and numbers are shown at the top of the panels.



the nutricline were higher on Hamilton Bank than on Saglek Bank.

Phosphate concentrations show a geographical and vertical pattern similar to that of nitrates. The only important difference is the presence of relatively high phosphates in the mixed layer at nearshore stations off, and south of, Hamilton Bank. This is most likely associated with the influence of the freshwater outflow from Hamilton Inlet. Silicates show a much more uniform distribution over the entire shelf, although there are higher values near Hudson Strait as well as along the shelf edge off Saglek and Nain banks.

Chlorophyll *a*

The highest depth-averaged chlorophyll *a* levels (>3 μg·L^{-1}) over the top 50 m were observed in the north over Saglek Bank (Fig. 4*b*). These elevated levels appear to extend south from here onto the northeast portion of Nain Bank and along the continental shelf break to Hopedale Saddle. There appears to be upwelling of nutrients into the saddles surrounding Okak Bank just north of Nain Bank. Isolated chlorophyll *a* patches of >1 μg·L^{-1} occurred off the northeastern edge of Harrison Bank and in the marginal trough inshore of Hamilton Bank. These distributions correspond to or are adjacent to regions of high nutrient concentrations (Fig. 4*a*). On Saglek and Nain banks, chlorophyll *a* levels tended to be highest over the central regions of the banks (Figs. 4*b* and 5*c*), whereas further south the maximum was shifted towards the continental slope (Fig. 4*b*). Along the Hamilton Bank transect, the chlorophyll *a* levels were maximum over the marginal trough adjacent to the inshore slope of the bank (Fig. 5*d*). In the vicinity of Hamilton Bank, maximum levels were also located below the pycnocline, in contrast with Saglek Bank where the chlorophyll *a* concentrations were maximum near the surface (Figs. 5*c* and 5*d*). The high chlorophyll *a* levels found in the north over Saglek and Nain banks were also present when depth integration was restricted to the upper mixed layer, but the elevated values near Harrison and Hamilton banks disappeared in the upper mixed layer integration. This is because most of the chlorophyll *a* at these sites lies primarily below the pycnocline. The mixed layer integration revealed relatively high values (>1 μg·L^{-1}) in the strongly stratified inshore waters south of Hamilton Inlet, however. This chlorophyll *a* was limited to very shallow depths, and thus was not prominent when the integration was taken over the top 50 m. Furthermore, the mixed layer integration revealed slightly enhanced chlorophyll *a* concentrations above the continental slope off eastern Hamilton Bank in association with relative

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Fig. 6. Contours of the biomass (g wet weight·100 m^{-3}) of (*a*) nanoplankton (1 to 8 µm), (*b*) microplankton (16 to <125 µm), (*c*) mesoplankton (125 to <1028 µm), (*d*) macroplankton (1028 to <4000 µm), and (*e*) nekton (4 to 16+ mm).

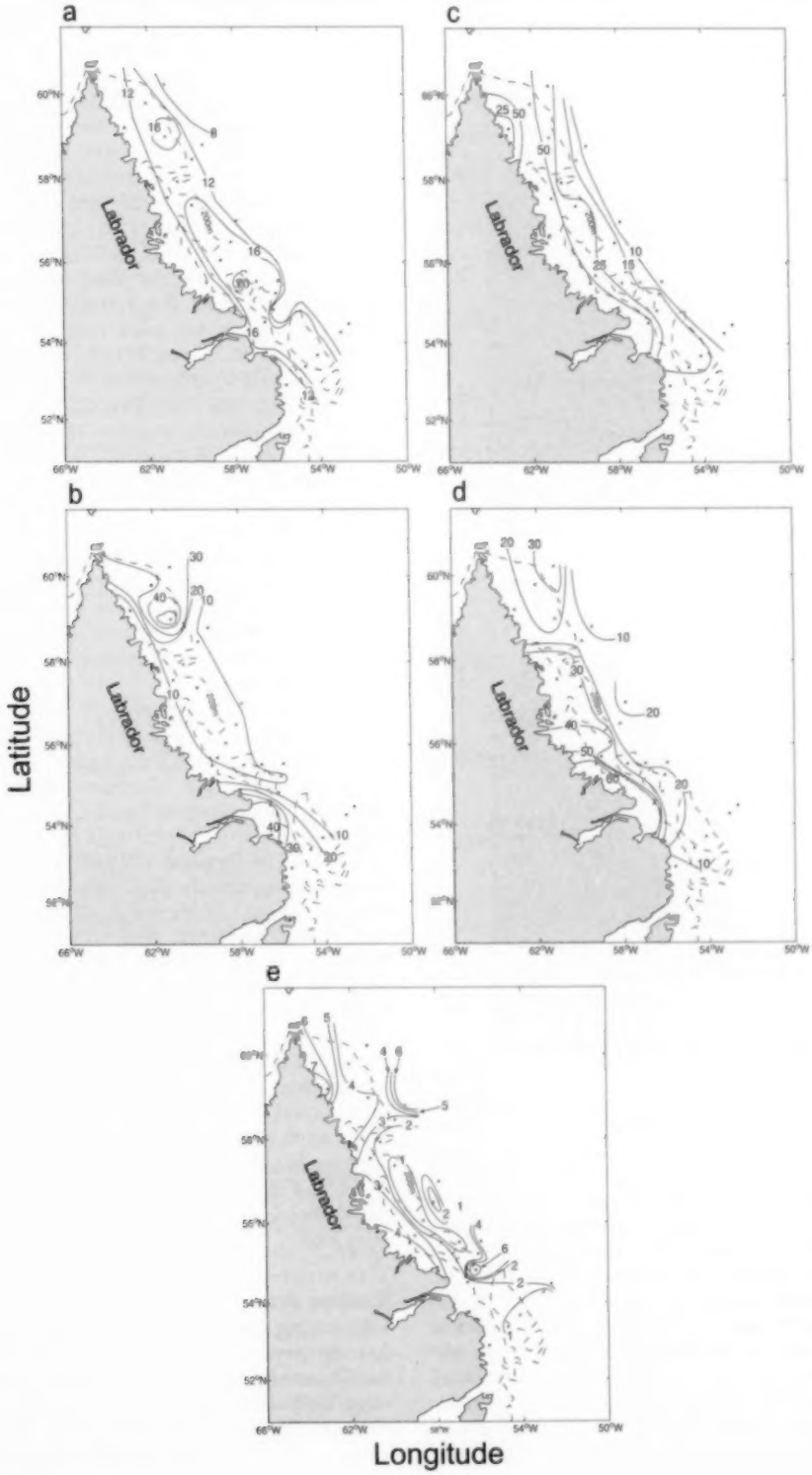

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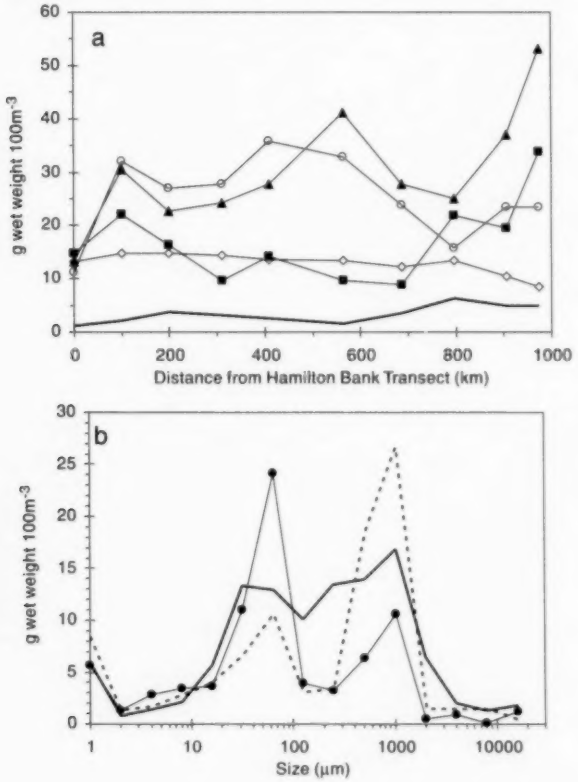
Fig. 7. (*a*) Average pelagic biomass across the Labrador Shelf of nanoplankton (diamonds), microplankton (squares), mesoplankton (triangles), macroplankton (open circles), and nekton (solid line without symbols) as a function of along-shelf distance from Hamilton Bank and (*b*) pelagic biomass size spectra from transects across Saglek Bank (solid line without symbols), Makkovik Bank (broken line), and Hamilton Bank (solid circles).



high nutrient levels (Fig. 5*b*), which also were not apparent from the upper 50 m depth-averaged values.

Biomass distributions

The biomass estimates of organisms from the Coulter-counted water and the size-fractionated net and trawl samples were amalgamated into five size-classes. These were 1–8 µm (nanoplankton, mostly small flagellates), 16 to <125 µm (microplankton), 125 to <1028 µm (mesoplankton dominated by small copepods), 1028 to <4000 µm (macroplankton consisting primarily of large copepods such as *Calanus*), and 4 to 16+ mm (nekton, which included crustaceans, fish larvae, and small fish). The time of day at which the larger zooplankters were captured could affect our biomass estimates because they are capable of daily migrations to depth during daylight (Crawford et al. 1992; Hudon et al. 1992). In our case the zooplankters would have to migrate to >300 m depth or close to the bottom at shallower stations to avoid our nets. Analysis of variance (on log + 1 transformed variables) in fact confirms that the nekton was undersampled during daylight ($p = 0.03$), but depth of water had no effect ($p = 0.6$). Time of day or depth of the water column did not significantly affect the biomass of other size categories, most notably macroplankton.

The ratio of the maximum to minimum station biomass over the shelf of the nano- and micro-plankton size categories, which are dominated by phytoplankters, was ~4 and 15 times, respectively. Nanoplankton distributions revealed relatively high values over the southern shelf area and in the north on Saglek Bank (Fig. 6*a*). There were maxima of over 20 g wet weight·100 m^{-3} to the north of Hamilton Inlet on Makkovik Bank (Station 24) and ~18 g wet weight·100 m^{-3} over Saglik Bank (Station 45) and a minimum in the offshore waters just north of 60°N of ~5 g wet weight·100 m^{-3} (Station 51). A stronger bimodal pattern dominated the microplankton, with concentrations in excess of 20 g wet weight·100 m^{3} in the north over and around Saglek Bank (Stations 45, 49, 51, and 54) and in the south in the marginal trough (Station 5) and inshore of Hamilton Bank (Stations 3 and 16) (Fig. 6*b*). This bimodal pattern of microplankton distribution roughly matches the chlorophyll *a* maxima (Fig. 4*a*), which is expected, since phytoplankton usually dominates the microplankton size group. However, the northern chlorophyll *a* maxima extended much farther south along the outer shelf to the southern tip of Nain Bank. The southern microplankton biomass distribution extended inshore beyond the inner Hamilton Bank through to a maximum near Hamilton Inlet (Fig. 6*b*). This divergence of chlorophyll *a* and microplankton distribution is not surprising given that microcrustaceans in this region make up >50% of the microplankton biomass.

The ratio of the maximum to minimum station biomass over the shelf of the meso- and macro-zooplankton size categories was ~18 and 58 times, respectively, much larger than for the phytoplankton. The mesoplankton, which was dominated by small copepod species such as *Pseudocalanus* sp. and *Oithona* sp., showed two distinct geographic trends (Fig. 6*c*). The first was a strong across-shelf gradient with higher values inshore that extended from Saglek Bank to Hamilton Bank. The second was a gradual southward decrease along the shelf from a maximum concentration of 72 g wet weight·100 m^{-3} near Hudson Strait. The macroplankton (primarily adult *Calanus* species) also showed a tendency towards decreasing biomass offshore over the central and southern Labrador Shelf (Fig. 6*d*). The maximum concentrations (50 g wet weight·100 m^{-3}) appeared inshore of Hopedale Saddle and Makkovik and Harrison banks. Nekton biomass was generally low, with minimum values in the extreme south of the study area. High values were found in the north on Saglek Bank, at some stations along the continental slope, and in the south in Cartwright Saddle (Fig. 6*e*). As stated above, this category suffers from a time of day sampling bias.

Biomass size spectra

If the hypothesis of an advective food chain is correct, then the relative importance of the larger sized organisms should increase southward. To test this, we calculated the average biomass for each size-class along the 10 cross-shelf transects. These were across Hamilton Bank (Stations 3–12), northern Hamilton Bank (Stations 12–16), Cartwright Saddle

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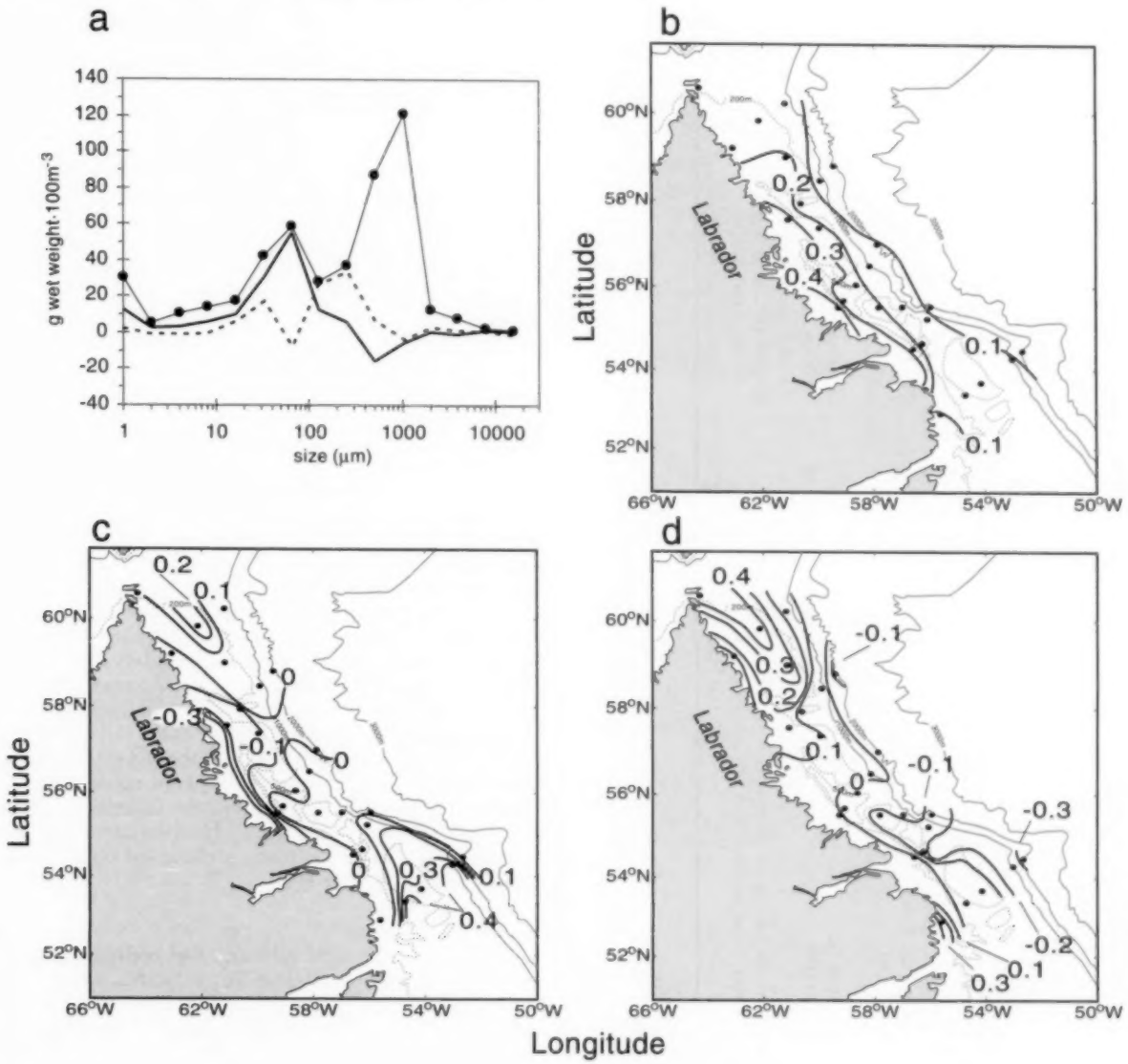
Fig. 8. (*a*) First (solid circles), second (solid thick line without symbols), and third (broken line) modes from the EOF analysis of the pelagic biomass size spectra over the Labrador Shelf, which account for 69, 13, and 9% of the total variance, respectively, and the spatial structure of the eigenvectors for the (*b*) first, (*c*) second, and (*d*) third modes.



(Stations 16–21), Makkovik Bank (Stations 21–26), Hopedale Saddle (Stations 26–32), Nain Bank (Stations 32–37), Okak Bank (Stations 37–42), southern Saglek Bank (Stations 42–47), central Saglek Bank (Stations 47–51), and the northern edge of Saglek Bank (Stations 51–54). The midpoint of each transect was used to calculate an along-shelf distance starting from the Hamilton Bank transect. The transect-averaged biomass for each of the five size-classes was then plotted against the along-shelf distance (Fig. 7*a*). The distance from Hamilton Bank to Hudson Strait is ~1000 km. The nanoplankton showed little spatial variability over the shelf but had a tendency for higher values to the south. The microplankton biomass suggests a bimodal distribution in the along-shelf direction with maxima towards the north and south, consistent with Fig. 6*b*. Mesoplankton biomass was maximum at the northernmost transect with lesser maxima over Nain and Hamilton banks. Macroplankton biomass had maxima at midshelf and to the south over the Hamilton Bank transect. Nekton biomass was relatively low throughout but with slight peaks near Harrison Bank in the south and over Saglik Bank in the north.

The biomass as a function of the logarithm of the size, i.e., the biomass size spectra, is plotted for three transects, Hamilton Bank in the south, Makkovik Bank in the central

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Table 1. Dominant taxa in the four community–hydrographic areas.

Plankton size category	Inshore Labrador Current (inner shelf)	Transitional (outer shelf, banks, and saddles)	Offshore Labrador Current (shelf edge)	Labrador Sea (slope)
Microplankton 16 to <125 µm	*Thalassiosira* sp., *Coscinodiscus* sp., *Peridinium* sp.	*Nitzchia* sp., *Coscinodiscus* sp.	*Rhizosolenia* sp., *Limacina* sp.	*Ceratium* sp., *Globigerina* sp., "tintinids"
Mesoplankton 125 to <1028 µm	*Pseudocalanus* sp.	*Pseudocalanus* sp.	*Limacina helicina*	*Oithona similis*
Macroplankton 1028 to <4000 µm	*Calanus glacialis*	*Calanus hyperboreus*, *Themisto* sp.	*Euchaeta glacialis*, *Euchaeta norvegicus*	*Calanus finmarchicus*, *Metridia longa*
Nekton 4 to 16+ mm	*Thysanoessa raschii*, *Liparis fabricii*, *Mysis mixta*, *Themisto libellula*, *Limacina helicina*	*Pseudolibrotis glacialis*, *Gadus morhua*, *Themisto compressa*, *Clione limacina*, *Aglanthe digitale*	*Meganyctiphanes norvegicus*, *Thysanoessa inermis*, *Reinhardtius hippoglossoides*	*Benthosema glaciale*, *Onychoteuthis banski*, *Myctophum punctatum*

Fig. 9. Contours of percent biomass of adult and stage V copepodites of (*a*) *Calanus glacialis* and (*b*) *Calanus finmarchicus* collected on a 1000-µm sieve from 460 µm mesh net tows, (*c*) *Calanus hyperboreus* and (*d*) *Euchaeta norvegicus* and *Euchaeta glacialis* combined collected on a 2-mm sieve from a Vass–Tucker trawl, and (*e*) *Pseudocalanus* sp. copepodite stages I–IV and (*f*) stage V and adults collected on a 250-µm sieve from 73 µm mesh net tows.

shelf area, and the central Saglek Bank in the north (Fig. 7*b*). In the north, there was relatively high biomass of phytoplankton (microplankton) through to zooplankton (meso- and macro-plankton). At Makkovik Bank, there was a shift towards a higher biomass of both the meso- and macroplankton size categories but much reduced phytoplankton biomass. On Hamilton Bank, the phytoplankton size categories dominated the particle spectra with low biomass of zooplankton.

An EOF analysis was carried out to further examine the spatial variability of the biomass size spectra. Over 90% of the total variance in the spectra was accounted for by the first three EOF modes. These modes and their eigenvectors are shown in Fig. 8. The first mode, which accounted for 69% of the total variance, had a dominant peak between the mesoplankton and macroplankton categories with a lesser peak in the microplankton size range (Fig. 8*a*). Spatially, the maximum amplitude lies inshore at midshelf with a strong cross-shelf gradient (Fig. 8*b*). The second mode accounted for 16% of the total variance and consisted of a peak in the microplankton category with a trough in the mesoplankton. The second mode eigenvectors show relatively high amplitudes in the north and the south with negative values at midshelf in the inshore region and over Nain Bank (Fig. 8*c*). The third mode accounted for only 8% of the variance. It has a peak in the spectra at the microplankton and mesoplankton categories (Fig. 8*a*) and spatially has high eigenvector amplitudes in the north (Fig. 8*d*). Positive eigenvectors were also found inshore at the southern end of the Labrador coast, while negative values were found offshore and on the southern half of the Labrador Shelf.

Species distributions

Four communities were identified that correspond to the main oceanographic features of our study area, which from offshore to inshore were the Labrador Sea, the offshore Labrador Current along the slope, a transitional zone (called the "Polar Front" by Conover et al. 1995), and the inshore Labrador Current. Each region contains distinctive dominant taxa from all trophic levels from the microplankton to nekton categories (Table 1). It is not intended to suggest that these community classifications are mutually exclusive. On the contrary, there is considerable exchange of species between the inner and outer shelf as exemplified by the distributions of the three *Calanus* sp. (Figs. 9*a*, 9*b*, and 9*c*). Furthermore, there is convincing distributional evidence that incursions of deeper water and associated biota occur through the outer saddles into the inner shelf basins, most notably from the microplankton (e.g., *Rhizosolenia* sp. and *Paraflavella* sp.) to nekton size categories (e.g., *Euchaeta* sp. and *Thysanoessa* sp.) (Fig. 9*d*). Only on the northern half of Saglik Bank are deepwater organisms, including nekton, reg-

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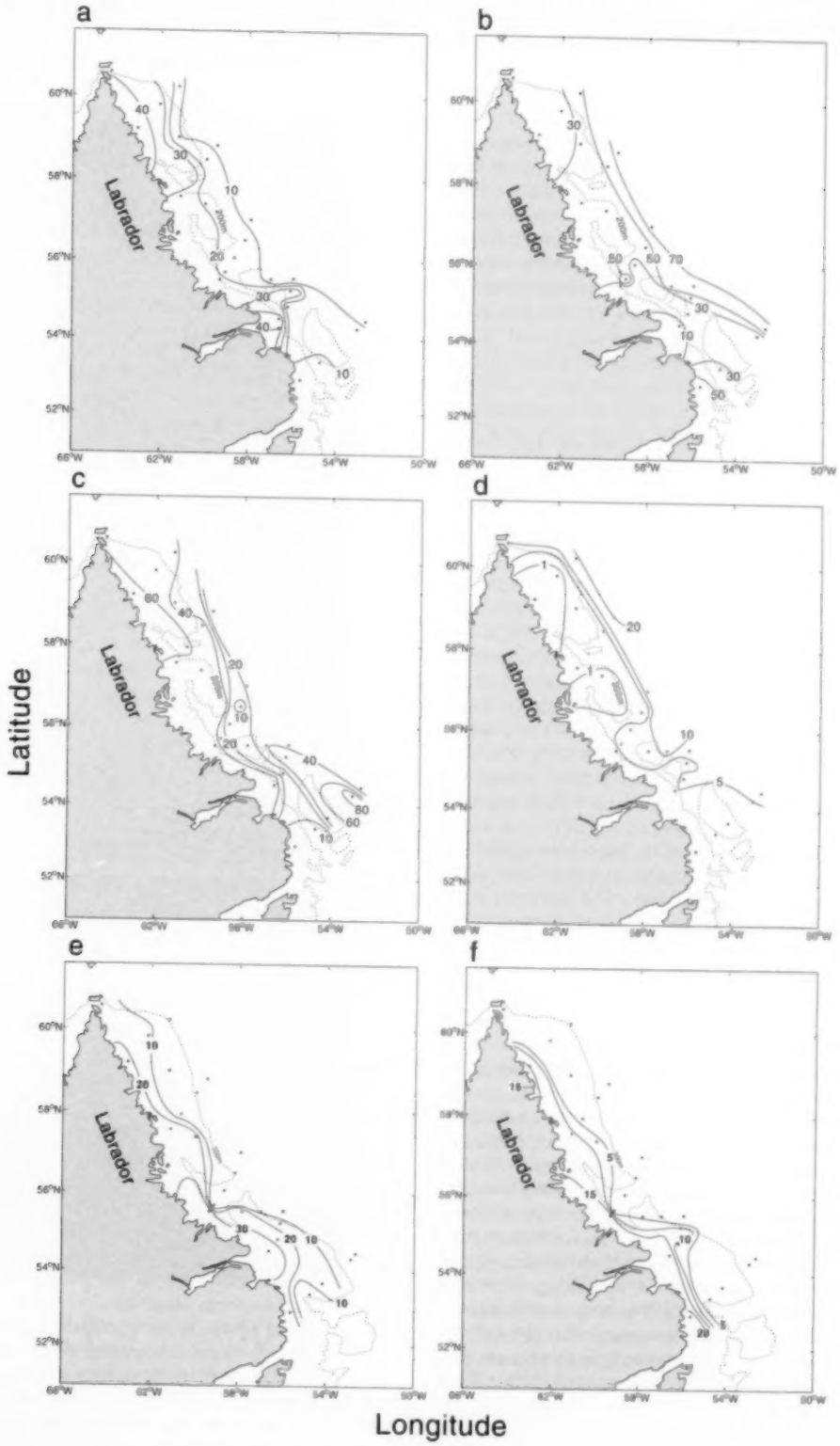

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ularly found over shallow water, which is believed to be a result of the turbulent tidal mixing near Hudson Strait and subsequent advection onto the bank.

The distributions of the developmental stages of the dominant mesoplankton copepod *Pseudocalanus* sp. were grouped into two categories to determine if there was an indication of a southward movement with progressively later life stages, as would be expected with an advective food chain. No significant difference in distribution was observed between the early stage copepodites (I–IV) and later stages (V–VI) (Figs. 9*e* and 9*f*). The same conclusion can be drawn from the distributions of the developmental stages of the arctic zooplankter *Calanus glacialis*.

Discussion

The low degree of stratification and high nutrient content on the northern Labrador Shelf measured during our September cruise reconfirm the effect of the Hudson Strait outflow on the physical and chemical properties of these waters (e.g., Kollmeyer et al. 1967; Lazier 1982; Colbourne and Mertz 1998). The high chlorophyll *a* concentrations and microplankton biomass indicate that increased primary production had occurred on the northern Labrador Shelf in response to the nutrient flux from Hudson Strait, consistent with the first hypothesis of Sutcliffe et al. (1983). Evidence that our results were representative of summertime conditions and not unique to the time of our cruise comes from satellite imagery of ocean colour. NASA's Coastal Zone Colour Scanner (CZCS) was operational between 1978 and 1986 and thus overlaps with the time of our study. The scanner sensed and calculated a weighted average of the relative phytoplankton biomass over approximately the upper 10 m of the water column (Sathyendranath and Platt 1989). The ocean colour images were averaged to obtain monthly composite images for each of the nine years as well as over all of the years combined (G. Harrison, Bedford Institute of Oceanography, Box 1006, Dartmouth, NS B2Y 4A2, Canada, personal communication). The monthly composites confirm that during the summer (July, August, and September), the highest near-surface phytoplankton biomass over the Labrador Shelf tends to be on the northern Labrador Shelf (Fig. 10).

High concentrations of phytoplankton, as measured by chlorophyll *a*, were also observed during our cruise near the inshore edge of Hamilton Bank, over Nain Bank, and along the shelf break. Most of the phytoplankton chlorophyll *a* at the former was located near the bottom of the pycnocline at about 30–50 m and in contrast with our observations on Saglek Bank where the highest concentrations were found in the upper 20 m or less. This peak in phytoplankton near Hamilton Bank was situated in a region of shallowing sigma-*t* and nutrient isopleths, indicative of upwelling. The high chlorophyll *a* levels off Hamilton Bank were not observed in the satellite colour imagery because they were beyond the depth range of the sensor. The relatively high primary production observed along the shelf break and outer Nain Bank also appears to be related to locally induced upwelling. These areas of high chlorophyll *a* are in close proximity to areas of relatively higher nitrate concentrations, which indicates ongoing production rather than a previous phytoplankton bloom settling out.

Does the high phytoplankton biomass on the northern Labrador Shelf support increased zooplankton production further downstream as predicted by the advective food chain hypothesis? The macroplankton biomass, consisting mostly of large copepods (*Calanus* sp.), increased downstream of Saglek Bank, near Nain Bank, and particularly in the more southern inshore regions of the shelf, consistent with the advective hypothesis. There was a relatively high standing crop of both micro- and mesoplankton on Saglek Bank but little evidence of a progressive gradient of zooplankton sizes being transported southward towards Hamilton Bank at this time of the year. The development times of many of the larger zooplankton (macroplankton) are of the order of 1–2 years (Grainger 1959; Cairns 1967), whereas the transit time of the shelf water based on the salinity signature is 2–3 months (Myers et al. 1990). It is most likely that macrozooplankters are feeding opportunistically in summer, with their major growth accrued from feeding upon the spring bloom as the ice retreats from the Labrador Shelf in May and June. Satellite imagery does show evidence of a chlorophyll *a* bloom as the ice retreats through the late spring and early summer.

Data collected on nekton abundance are less reliable than for the other size-classes quantified because they can migrate vertically to near the bottom during the day and therefore were not consistently sampled. In spite of this complication, there was a clear distributional pattern in biomass on the shelf, from high values (>4 g wet weight·100 m^{-3}) in the north over Saglek Bank and at some locations along the shelf margin to low values (<2 g wet weight·100 m^{-3}) farther south over the banks. The high nekton concentrations near the shelf break were due mainly to large catches of mesopelagics such as lantern fish, euphausiids, shrimps, etc. These nekton were probably supported by a local food chain based on phytoplankton production at the edge of the shelf. There is also evidence from this biomass distribution that higher shelf-break nekton concentrations penetrate or might be continuous with the inner shelf basins through the Hopedale and Cartwright saddles.

The advective food chain hypothesis of Sutcliffe et al. (1983) suggested that nutrient-induced production is advected via the food chain along the Labrador Shelf to Hamilton Bank and eventually onto the northern Newfoundland Shelf. Although our data show that the peak in the macroplankton biomass does appear downstream of the highest primary production on Saglek Bank, the hypothesis is not strongly supported by the distribution of other size categories. First, an inverse relationship existed between nearshore meso- and micro-plankton biomass concentrations. We interpret this as meaning that the small copepod community, dominated by *Pseudocalanus* sp., had grazed down their prey, the microzooplankton, by the time of our cruise. Moreover, this inverse relationship was observed over the entire shelf with no indication that it was being established progressively as the organisms were being transported down the shelf. Second, the zooplankton biomass in various size categories on Hamilton Bank and vicinity at the time of our collections was relatively low. This low biomass could possibly be explained by increased predation; however, all trophic levels were pres-

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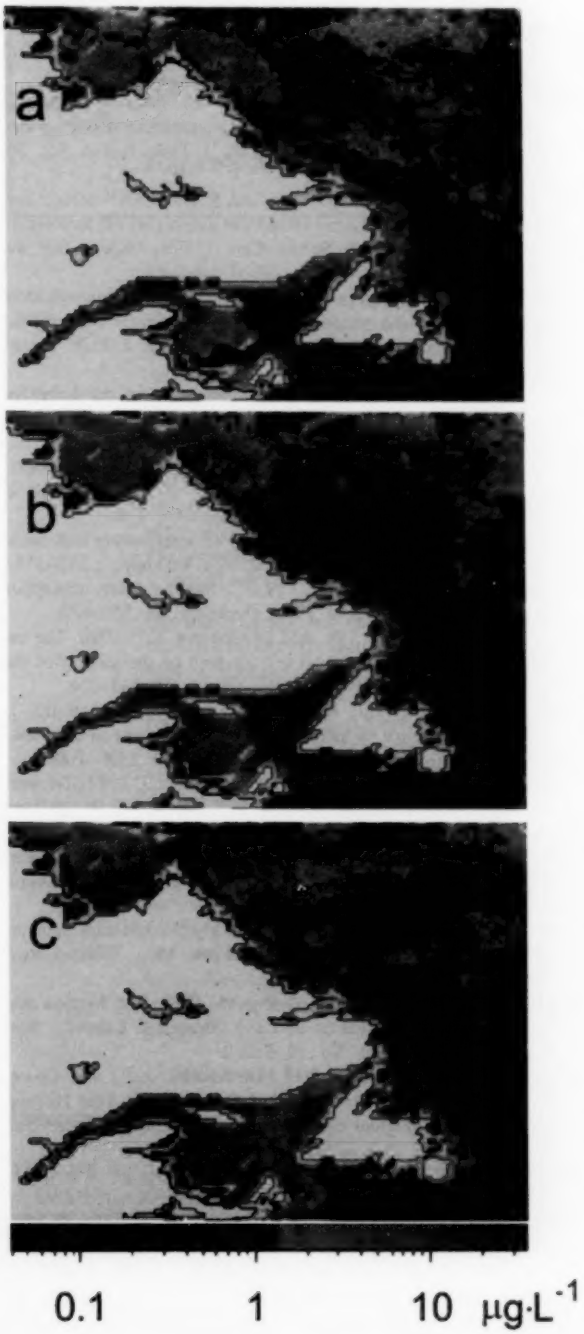
Fig. 10. Composite colour imagery of chlorophyll *a* concentrations estimated from the CZCS sensors for (*a*) July, (*b*) August, and (*c*) September averaged for the years 1978–1986. Note the high concentrations (red) on the northern shelf in all three months.



ent at low levels including the nekton that feeds upon the larger zooplankton. Third, there was relatively high abundance of zooplankton biomass on the northern Labrador Shelf, which was not predicted under the advective hypothesis. Finally, development stages of the various dominant copepod species, such as *Pseudocalanus* and *Calanus*, showed no evidence of a gradual distribution shift southward with increasing age.

How could the observed high zooplankton biomass be maintained over Saglek Bank? Sutcliffe et al. (1983) assumed a southward flow over the entire shelf and at the shelf break. More recent current meter observations show that the residual currents on the banks, including Saglek, are relatively weak (Fissel and Lemon 1991). This implies a longer residence time for the water and organisms on the banks compared with the water inshore, in the marginal troughs, or along the continental slope. This is supported by the geographic distributions reported here of a wide size range of organisms of various swimming abilities. Residence times of 1–2 months on the banks are of sufficient duration for micro- and meso-plankton to develop locally. Direct advection of zooplankton from Hudson Strait may also contribute to the high zooplankton abundance on Saglek Bank judging from the number of deepwater species found there. Saglek was the only bank on the entire Labrador Shelf where such species were observed.

One of the main objectives of Sutcliffe et al. (1983) was to explain the greater fish biomass and production on the southern Labrador and northern Newfoundland Shelf. If a large-scale advective food chain propagating southward over the Labrador Shelf does not exist, what does support the higher fish production in the south? Much of this production occurs in the vicinity of Hamilton Bank and until recently consisted primarily of Atlantic cod. The cod feed upon capelin (*Mallotus villosus*), which in turn prey upon smaller fish and large zooplankters. This food chain could have been supported by local spring phytoplankton production, followed by that generated by upwelling processes at both the shelf break and in the marginal trough at the inshore edge of Hamilton Bank. Our observations of nutrients, chlorophyll *a*, and phytoplankton biomass are consistent with this scenario. There was also high phytoplankton biomass in the very near-surface waters inshore off Hamilton Inlet, which is attributed to the effects of local freshwater runoff.

On the basis of hydrographic, nutrient, chlorophyll *a*, and biomass size spectra collected on the Labrador Shelf during September 1985, we have reached the following conclusions. The mean outflow from Hudson Strait carries nutrient-enriched waters to the northern Labrador Shelf, which results in sustained phytoplankton production and high standing stocks throughout the summer. This production supports local zooplankton production on Saglek Bank, although some unknown quantity of zooplankton was also advected onto the Bank from Hudson Strait based on the presence of expatriated deepwater species. Evidence does not support the hypothesis that most of this production is advected southward forming a "conveyor belt" food chain, as proposed by Sutcliffe et al. (1983). Peak mesoplankton and macroplankton biomass concentrations, however, do extend downstream of Saglek Bank, particularly at the inner shelf stations from Nain to Hamilton Inlet. Individual species distributions of the main community types do indicate southward flow along the inner shelf and along the shelf break by the Labrador Current,

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but their developmental stage distributions do not support a progressional transport of production south at the correct time scale. The high fish production observed historically in the vicinity of Hamilton Bank was most likely a result of response to local upwelling and primary production processes.

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ARTICLES

Variations in the isotope composition of mercury in a freshwater sediment sequence and food web

Togwell A. Jackson

Abstract: Analysis of a sediment core and food-web animals from the Niagara Basin of Lake Ontario yielded the first recorded evidence for systematic variations in the stable-isotope composition of mercury (Hg) in natural environments on Earth. The sediments comprised younger strata enriched in Hg by recent pollution overlying older strata containing background Hg only. Several Hg isotope ratios, including $^{199}Hg/^{201}Hg$, $^{201}Hg/^{204}Hg$, and $^{202}Hg/^{204}Hg$, varied significantly with the Mn/Fe ratio of the extractable readily reduced oxyhydroxide fraction of the sediment and with the concentrations of extractable Mn or Fe fractions, or both, in the sediment, and the zone of recent Hg pollution gave strikingly different results than the zone of background Hg. Food-web animals displayed a progressive increase in the $^{202}Hg/^{204}Hg$ ratio from lower to higher trophic levels in the order crustaceans < forage fish < trout; but superimposed on this trend were secondary trends owing to systematic decreases in the ratio from planktonic to benthic crustaceans and, correspondingly, from plankton-eating to benthos-eating forage fish. The results of the research suggest fractionation of Hg isotopes by natural processes, including Hg methylation, with effects linked to temporal variations in the oxidation-reduction potential of the sediments. These findings show that Hg isotopes could provide valuable but as yet untapped information about the sources and biogeochemical cycling of natural and anthropogenic Hg.

Résumé : L'analyse d'une carotte sédimentaire et l'étude des animaux du réseau trophique du bassin Niagara, dans le lac Ontario, ont mis pour la première fois en évidence des variations systématiques de la composition des isotopes stables du mercure (Hg) dans les milieux naturels de la Terre. Les sédiments se composaient de strates jeunes enrichies en Hg par la pollution récente, qui recouvraient des strates plus anciennes présentant seulement une concentration de fond de Hg. Plusieurs rapports des isotopes de Hg, notamment $^{199}Hg/^{201}Hg$, $^{201}Hg/^{204}Hg$ et $^{202}Hg/^{204}Hg$, variaient de façon significative avec le rapport Mn/Fe de la fraction oxyhydroxide extractible et facilement réduite du sédiment, et avec les concentrations des fractions extractibles de Mn ou de Fe, ou avec les deux, dans le sédiment, et la zone présentant une pollution récente par Hg donnait des résultats remarquablement différents de ceux de la zone ne présentant qu'une concentration de fond de Hg. Les animaux du réseau trophique présentaient une augmentation progressive du rapport $^{202}Hg/^{204}Hg$ lorsqu'on passait des niveaux trophiques les plus bas aux niveaux les plus hauts dans l'ordre crustacés < poissons fourrage < truite; mais à cette tendance venaient se superposer des tendances secondaires liées aux baisses systématiques du rapport des crustacés planctoniques aux crustacés benthiques et, en parallèle, des poissons fourrage planctivores aux poissons benthivores. Les résultats de la recherche permettent de penser que les isotopes de Hg sont fractionnés par des processus naturels, notamment la méthylation, et ont des effets liés aux variations temporelles dans le potentiel oxydoréducteur des sédiments. Ces constats montrent que les isotopes de Hg pourraient fournir une information précieuse mais encore inexploitée sur les sources et le cycle biogéochimique du Hg naturel et anthropique.

[Traduit par la Rédaction]

Introduction

Mercury in the environment

The contamination of ecosystems with mercury (Hg) is a serious, widespread problem (Jackson 1997, 1998*a*; Fitzgerald et al. 1998). In aquatic environments, Hg, mostly in the form of inorganic Hg(II), is concentrated in fine-grained sediments and is partly converted to the highly toxic, relatively bioavailable species methyl Hg (CH_3Hg^+) by microorganisms. CH_3Hg^+ is readily accumulated by organisms and, unlike inorganic Hg(II), it undergoes biomagnification from lower to higher trophic levels, becoming preferentially concentrated in fish.

Since the onset of industrialisation, Hg introduced into the environment from various sources of pollution has greatly augmented the Hg released from natural sources (Jackson 1997, 1998*a*, 1998*b*). Some of this Hg is discharged directly into natural waters (usually rivers) and may be transported to lakes or the sea by fluvial action. Major quantities of Hg are also released into the atmosphere and are transported by winds to ecosystems up to several thousand kilometres away

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(Jackson 1997; Fitzgerald et al. 1998). Consequently, cores of continuous undisturbed sequences of fine-grained lake sediments, which provide historical records of Hg deposition, commonly show Hg enrichment in the upper (younger) strata, with lower Hg concentrations in the lower (older) strata. This tendency, accompanied by anomalously high CH_3Hg^+ levels in fish under conditions particularly favourable for the production and bioaccumulation of CH_3Hg^+, is found in virtually pristine lakes far from known sources of pollution, as well as in lakes polluted with Hg from local sources. Typically, the Hg concentration increases progressively upward to the sediment–water interface, implying that the rate of anthropogenic Hg deposition has been rising unchecked over time, or else increases to a maximum and then declines, indicating the occurrence of Hg pollution followed by abatement of the pollution (Engstrom and Swain 1997; Jackson 1997). Although there is general agreement on the broad features of the biogeochemical cycle of Hg and on the interpretation of Hg profiles in cores, the Hg cycle is somewhat clouded by uncertainties, owing to its complexity and, in contaminated ecosystems far from the sources of contamination, the difficulty of identifying and quantifying contributions from specific sources. Natural and anthropogenic Hg from a variety of primary and secondary sources undergo mixing, cycling, and recycling in the environment. Once Hg has been dispersed in the environment, attempts to differentiate between the effects of different sources and to disentangle the separate histories of the different Hg atoms brought together at a particular locality are rather problematic, except in the vicinity of a known point source, although in remote regions, where the uncertainty is greatest, reasonable inferences may be drawn from various lines of evidence, such as spatial and temporal trends (Jackson 1997; Fitzgerald et al. 1998). Variations in the stable-isotope composition of Hg could conceivably provide important but hitherto unknown information on the sources and biogeochemistry of Hg in natural environments. The purpose of the author's research was to investigate this possibility.

Stable isotopes of Hg and other elements

Owing to their different atomic and molecular weights, the stable isotopes of an element and simple compounds of these isotopes, respectively, differ somewhat in their physicochemical properties (e.g., rates of evaporation, reaction rates, and binding energies), and these isotope effects are influenced by environmental variables, such as temperature and pH (Rankama 1956, 1963; Hoefs 1973). The differences in properties, though generally small, may lead to isotope fractionation by physicochemical and biological processes. Separation of isotopes in complex natural environments is apt to be the net effect of several different processes. Some of these phenomena may have additive effects, while others may tend to cancel each other's effects, and the overall result may be hard to predict or interpret (Rankama 1956, 1963). Natural fractionation of isotopes has provided important information about the sources, biogeochemical cycling, and geological history of various elements, in particular the lighter ones, such as C, H, O, N, and S (Rankama 1956, 1963; Hoefs 1973). The tendency of stable isotopes to be separated by natural processes decreases sharply, however, with increasing atomic mass and is thought to be negligible for the heavier elements, such as Hg, because the isotopes differ so little from one another in mass (Rankama 1956; Hoefs 1973). Nevertheless, measurable systematic variations in the isotope composition of relatively heavy elements are theoretically possible, especially since a series of small effects can lead to a greatly amplified overall effect in nature (Rankama 1956).

Hg has seven stable isotopes, the atomic weights and conventional percent abundances of which are ^{196}Hg (0.146%), ^{198}Hg (10.02%), ^{199}Hg (16.84%), ^{200}Hg (23.13%), ^{201}Hg (13.22%), ^{202}Hg (29.80%), and ^{204}Hg (6.85%) (Bainbridge and Nier 1950; Rankama 1956). Appreciable separation of Hg isotopes has been achieved experimentally by evaporation and distillation, by effusion, and by the action of an electric current (Brönsted and von Hevesy 1921; Mulliken and Harkins 1922; Haeffner 1953). This implies that certain natural and industrial processes may lead to the fractionation of Hg isotopes and that the isotope composition of Hg could depend to some extent on the source of the Hg (Rankama 1956, 1963). In theory, fractionation of Hg isotopes at sources of contamination and in the environment could give rise to small systematic spatial and temporal variations in the isotope composition of Hg in natural environments. If so, measurements of Hg isotope ratios performed with sufficiently precise and sensitive instruments could be used to distinguish between different sources and biogeochemical pathways of Hg in ecosystems. However, with the exception of several papers on the supposed occurrence of Hg isotope anomalies in meteorites and moon rocks (Jovanovic and Reed 1990; Kumar and Goel 1992*a*, 1992*b*) and an early report of an unsuccessful attempt to detect differences in the isotope content of Hg ore samples from different deposits (Brönsted and von Hevesy 1922), there appears to be no published evidence for or against the occurrence of significant variations in Hg isotope ratios in nature, nor any mention of attempts to obtain such information. Here, evidently for the first time, systematic variations in the stable-isotope composition of Hg in a sediment sequence and associated food web are demonstrated. The abstract of an oral presentation on this work has been published elsewhere (Jackson 1999).

Materials and methods

The Niagara Basin of Lake Ontario was selected for study because it is polluted with Hg from industrial point sources along the Niagara River, which flows into the basin (Mudroch 1983; Thomas 1983; Whittle and Fitzsimons 1983). A mini box core of fine-grained profundal sediment was collected from the basin in August 1996. From this, a second core was taken by hand, stored at 4°C, and, in the spring of 1998, cut into 1-cm sections and analyzed.

Portions of the core sections were analysed in duplicate for total Hg by extraction with H_2SO_4/HNO_3 (2:1, v/v) at 60°C, addition of $KMnO_4$, $K_2S_2O_8$, and H_2SO_4, reduction of Hg(II) to Hg(0) by $SnCl_2$, and determination of the Hg(0) by cold vapour atomic absorption spectrophotometry (AAS). The Hg isotope content of each extract was then determined in triplicate by the reduction of Hg(II) to Hg(0) with $SnCl_2$, and analysis of the Hg(0) by inductively coupled plasma quadrupole mass spectrometry (ICP-MS), using a VG Elemental PQ2+ ICP-MS system, with argon as the carrier gas. Thus, a total of six replicate sets of data were obtained for each core section. The isotopes ^{198}Hg, ^{199}Hg, ^{200}Hg, ^{201}Hg, ^{202}Hg, and ^{204}Hg were determined, but ^{196}Hg was omitted, because it was not abundant enough to be measured with sufficient accuracy and precision. Hg isotope composition was expressed as a series of simple

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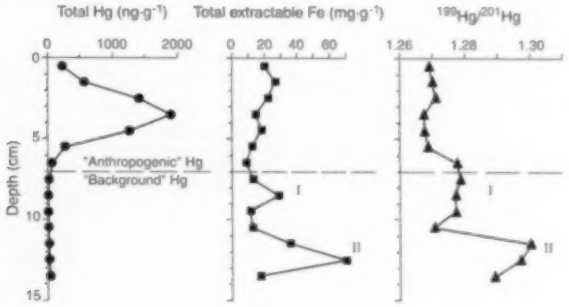
Fig. 1. The vertical profiles of total Hg, total extractable Fe, and the $^{199}Hg/^{201}Hg$ ratio in the sediment core from the Niagara Basin of Lake Ontario.



isotope ratios. A solution of high-purity Hg(0) (99.98% source purity) (High Purity Standards, Charleston, South Carolina) was used to calibrate the system and to correct the data for any inherent mass bias effect, on the assumption that the proportions of the isotopes in the pure metal were the same as those reported in the literature (Bainbridge and Nier 1950; Rankama 1956). The precision of each isotope ratio was calculated from replicate measurements of the concentration ratios of the standard; the relative standard deviation and 99% confidence limits can be provided on request. A standard solution of Hg(II) was analysed at intervals throughout the course of the sample analyses, to check for possible systematic errors caused by drift of the readings in a preferred direction over time.

In addition, duplicate subsamples of the core sections were extracted sequentially with $NH_2OH{\cdot}HCl/HNO_3$, $H_2O_2/HNO_3/NH_4$ acetate (Ac), and citrate/dithionite, in that order, to isolate the easily reduced "amorphous" (short-range order) oxyhydroxides, organically bound species, and less easily reduced "crystalline" (long-range order) oxyhydroxides, respectively, of Fe and Mn (Gupta and Chen 1975). The extracts were then analysed for Fe and Mn by AAS and for Hg by cold vapour AAS. The core sections were also subjected to radiometric dating, employing the ^{210}Pb method (Eakins and Morrison 1978; Turner 1990).

The biological samples consisted of planktonic and benthic crustaceans, forage fish that feed on these invertebrates, and trout, which prey on the forage fish. The specimens were collected from the Niagara Basin in August and September 1998, whereupon they were frozen, homogenised, and analysed for total Hg and Hg isotope content by the techniques used for analysis of the sediments. Single samples of the crustaceans and duplicate samples of the fish were each analysed in duplicate. As with the core sections, a standard solution of Hg(II) was analysed at intervals during the course of the isotope analyses.

Ten replicate portions of a sample of pulverised cinnabar from the Almaden Hg mine in Spain were analysed as well, for the purpose of estimating the precision of the techniques used to measure the Hg isotope ratios and for the sake of obtaining reference data for comparison with the data for the core sections and biological samples.

In all plots and regression analyses involving sediment data, the average values of the Hg isotope ratios for each core section were expressed as medians rather than means, to minimise distortion due to extreme values. Averages for biological samples, however, were expressed as means, because three of a total of seven specimens were analysed in duplicate only. Similarly, all chemical data had to be expressed as mean values, because the analyses were done in duplicate.

Table 1. The total Hg concentrations and ^{210}Pb dates of consecutive 1-cm sections of the core from the Niagara Basin of Lake Ontario; the Hg concentrations are based on dry weight.

	Total Hg ($ng{\cdot}g^{-1}$)		
Depth (cm)	Mean	Range	^{210}Pb date
0–1	239.34	198.49–280.19	1989±16
1–2	566.68	496.18–637.18	1976±11
2–3	1420.785	1375.56–1466.01	1963±14
3–4	1886.65	1882.29–1891.01	1949±14
4–5	1264.1	1258.73–1269.4	1933±17
5–6	274.92	219.7–330.14	1916±18
6–7	70.01	61.77–78.25	1898±18
7–8	16.3	13.89–18.8	—
8–9	10.6	9.86–11.39	—
9–10	9.67	9.43–9.91	—
10–11	11.55	9.77–13.33	—
11–12	12.89	12.17–13.61	—
12–13	11.685	11.59–11.78	—
13–14	28.9	21.84–35.9	—

Results and discussion

The sediment core

Analysis of the core sections revealed striking systematic vertical variations in the total Hg and total extractable Fe content and the $^{199}Hg/^{201}Hg$ ratio of the sediment (Fig. 1; Tables 1–3) (total extractable Fe being defined as the sum of the three solvent-extractable Fe fractions, of which citrate/dithionite-extractable Fe was the most abundant (Table 3)). The $^{199}Hg/^{201}Hg$ ratio of the Hg standard solution (T.A. Jackson, unpublished data) showed only minor random fluctuation about a vertical line, demonstrating that there were no systematic errors caused by deviation in a preferred direction during the course of the sample analyses. Moreover, the ^{210}Pb measurements (Table 1) imply that the core data comprise an unbroken historical record. Thus, the ^{210}Pb ages increase progressively with depth, and the correlation of age with depth is highly significant ($r = 0.998$; $P < 0.001$), indicating continuous deposition at a virtually constant annual rate and the absence of postdepositional disturbance.

The total-Hg profile shows a large buried maximum representing Hg pollution from local sources, with consistently low background values below this zone of anthropogenic Hg enrichment (Fig. 1). The pollution began around 1898, became progressively worse until some time between 1949 and 1963, and then abated (Table 1). For convenience, the region of Hg enrichment and the underlying Hg-poor region are herewith designated as the zones of "anthropogenic" and "background" Hg, respectively (although this is an oversimplification, as the anthropogenic Hg of local origin is presumably mixed with background Hg comprising trace amounts of natural and anthropogenic Hg from various primary and secondary sources (Jackson 1997, 1998*a*)). The $^{199}Hg/^{201}Hg$ ratio is independent of total Hg, but its core profile parallels that of the total extractable Fe and citrate/dithionite-extractable Fe to a remarkable degree (Fig. 1; Tables 2 and 3). The $^{199}Hg/^{201}Hg$ ratio and Fe show little variation with depth in the zone of anthropogenic Hg but, in the zone of background

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Table 2. The $^{199}Hg/^{201}Hg$, $^{201}Hg/^{204}Hg$, $^{202}Hg/^{204}Hg$, $^{200}Hg/^{202}Hg$, and $^{198}Hg/^{204}Hg$ ratios of consecutive 1-cm sections of the core from

Depth	$^{199}Hg/^{201}Hg$				$^{201}Hg/^{204}Hg$			
(cm)	Median	Mean	SD	Range	Median	Mean	SD	Range
0–1	1.269	1.269	0.005574	1.264–1.276	1.945	1.946	0.01145	1.932–1.962
1–2	1.270	1.268	0.006802	1.259–1.276	1.9255	1.9265	0.005010	1.921–1.933
2–3	1.271	1.273	0.005279	1.269–1.281	1.9305	1.928	0.006306	1.916–1.933
3–4	1.2675	1.270	0.006831	1.262–1.278	1.949	1.948	0.007062	1.938–1.956
4–5	1.2675	1.267	0.003615	1.263–1.273	1.938	1.9375	0.003209	1.932–1.941
5–6	1.2685	1.268	0.005115	1.259–1.273	1.929	1.932	0.01665	1.914–1.958
6–7	1.2775	1.277	0.005879	1.270–1.284	1.930	1.930	0.009131	1.917–1.943
7–8	1.2785	1.277	0.01611	1.257–1.297	1.879	1.886	0.02165	1.861–1.919
8–9	1.277	1.279	0.01867	1.257–1.306	1.9105	1.917	0.02544	1.887–1.962
9–10	1.277	1.270	0.02049	1.234–1.289	1.9205	1.922	0.03744	1.874–1.974
10–11	1.2705	1.278	0.02283	1.258–1.316	1.9385	1.924	0.04636	1.843–1.969
11–12	1.300	1.303	0.01765	1.283–1.329	1.8895	1.895	0.03327	1.863–1.946
12–13	1.297	1.293	0.01374	1.273–1.311	1.876	1.8955	0.03939	1.864–1.952
13–14	1.284	1.286	0.008501	1.278–1.299	1.9115	1.921	0.02703	1.901–1.974

Note: The data are based on the results of six replicate analyses per core section (more precisely, triplicate analyses of duplicate extracts). SD is the

Hg (together with the lowest anthropogenic horizon (the 6- to 7-cm section), which borders it), they are each characterised by a small maximum overlying a much larger maximum (called peaks I and II, respectively). Unlike the other core sections, which were grey to brownish grey, the sections represented by peak I and, to a far greater extent, peak II were distinguished by a conspicuous yellowish brown colour, reflecting an anomalous abundance of Fe oxyhydroxide, as confirmed by the analytical data (Table 3).

As would be expected from the variations revealed in Fig. 1, the $^{199}Hg/^{201}Hg$ ratio of the background zone (combined with the adjacent basal section of the anthropogenic zone) gave a significant positive correlation with total extractable Fe ($r = 0.790$; $P > 0.01$, < 0.02); the anthropogenic zone, too, gave a positive correlation, although a much weaker one ($r = 0.696$; $P > 0.1$). However, a plot of the $^{199}Hg/^{201}Hg$ ratio against the Mn/Fe ratio of the $NH_2OH{\cdot}HCl/HNO_3$-extractable oxyhydroxide fraction yielded more significant and instructive results (Fig. 2; Tables 2 and 3). The Mn/Fe ratio of the $NH_2OH{\cdot}HCl/HNO_3$-extractable fraction of lake sediment tends to increase with the oxidation–reduction potential (Eh) of the sediment and the degree of aeration of the overlying water (Jackson 1988; Jackson and Bistricki 1995), reflecting the fact that, at any given pH, MnOOH precipitates at a higher Eh or dissolved O_2 concentration than does FeOOH (Degens 1965). The Mn/Fe ratio, therefore, is a useful index of sediment Eh at the time of deposition.

The plot of the $^{199}Hg/^{201}Hg$ ratio against the Mn/Fe ratio (Fig. 2) resolves itself into three highly significant trends representing the three principal regions of the core as defined thus far: the anthropogenic zone and the peak I and peak II segments of the background zone. Not surprisingly, the base of the anthropogenic zone (the 6- to 7-cm section), which has the lowest proportion of anthropogenic Hg to background Hg, falls on the peak I curve; it has, therefore, been treated as part of the peak I sequence of core sections. The two sets of background data yielded inverse correlations with separate but converging regression lines, and the point where the trends are joined represents, appropriately, the physical boundary between peaks I and II (the 10- to 11-cm section). In contrast, the anthropogenic zone gave a positive correlation, and the slope of the regression line is relatively low. Moreover, the regression line for the anthropogenic zone lies below both of the regression lines for the background zone. Thus the anthropogenic Hg is isotopically heavier than the background Hg, insofar as the $^{199}Hg/^{201}Hg$ ratio is concerned, with the sole exception of the 6- to 7-cm section and possibly the 10- to 11-cm section, which is a borderline case. Also note that the four oldest anthropogenic sections, which record the temporal increase in the severity of Hg pollution up to its maximum, have much lower Mn/Fe ratios than the three youngest sections, which record the subsequent decrease in the severity of Hg pollution over time (Fig. 2). This contrast in sediment chemistry suggests that these two regions of the anthropogenic zone represent quite different environmental conditions owing to their differences in pollution history.

For all three regions of the core, the Mn/Fe ratio of the $NH_2OH{\cdot}HCl/HNO_3$-extractable fraction gave much higher correlation coefficients (r values) and significance probabilities (P values) than the Mn or Fe concentration alone. Thus, P values for the Mn/Fe ratios range from <0.001 to >0.001, <0.01 (Fig. 2), but the values for Fe and Mn alone range from >0.02, <0.05 to >>0.1. This implies that the causes of the variations in Hg isotope composition are related to the environmental factors that determined the proportion of MnOOH to FeOOH at the time of deposition, whereas the abundance of MnOOH or FeOOH, in itself, is not necessarily important or even relevant. More specifically, the isotope ratio is probably a function of certain biogeochemical processes (possibly microbial activities) directly or indirectly linked to Eh. However, the marked differences between the three curves in Fig. 2 suggest that several different factors, which varied from one environment of deposition to another, determined the overall relationship between isotope ratio and Eh. Evidently each of the three zones in the sediment sequence represents a distinct environmental and biogeochemical regime with its own specific relationship between isotope ratio and Eh.

The radical differences between the results for the anthropogenic zone as a whole and the background zone as a whole might be supposed, at first glance, to result from the

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the Niagara Basin of Lake Ontario.

$^{202}Hg/^{204}Hg$				$^{200}Hg/^{202}Hg$				$^{198}Hg/^{204}Hg$			
Median	Mean	SD	Range	Median	Mean	SD	Range	Median	Mean	SD	Range
4.350	4.351	0.02209	4.325–4.384	0.7735	0.775	0.00327	0.771–0.780	1.4705	1.470	0.01009	1.454–1.480
4.302	4.300	0.01247	4.283–4.316	0.770	0.770	0.00151	0.768–0.771	1.4535	1.453	0.003327	1.448–1.458
4.343	4.340	0.01879	4.307–4.357	0.7655	0.765	0.00306	0.761–0.770	1.4435	1.4445	0.006535	1.434–1.452
4.381	4.386	0.01736	4.363–4.407	0.780	0.786	0.0241	0.763–0.820	1.4535	1.450	0.005317	1.443–1.454
4.345	4.343	0.01411	4.325–4.365	0.7635	0.763	0.00279	0.759–0.766	1.4425	1.444	0.004875	1.439–1.450
4.315	4.318	0.04436	4.261–4.369	0.774	0.774	0.00367	0.770–0.777	1.4555	1.457	0.01790	1.436–1.477
4.337	4.341	0.03686	4.290–4.401	0.7755	0.7755	0.00351	0.770–0.779	1.471	1.469	0.01280	1.452–1.487
4.262	4.269	0.03574	4.223–4.314	0.772	0.770	0.00728	0.758–0.779	1.437	1.440	0.01828	1.421–1.472
4.2865	4.303	0.07375	4.227–4.431	0.771	0.772	0.00769	0.762–0.783	1.4425	1.436	0.01898	1.407–1.455
4.313	4.335	0.09592	4.232–4.482	0.7735	0.775	0.0105	0.763–0.789	1.4425	1.449	0.02549	1.418–1.480
4.327	4.330	0.07582	4.212–4.427	0.7665	0.768	0.0116	0.756–0.785	1.461	1.454	0.03791	1.387–1.500
4.302	4.299	0.03801	4.252–4.352	0.7645	0.764	0.00739	0.754–0.774	1.4545	1.456	0.02911	1.416–1.494
4.297	4.306	0.07212	4.193–4.403	0.7665	0.766	0.00564	0.757–0.774	1.4265	1.433	0.02579	1.403–1.467
4.329	4.343	0.05223	4.284–4.439	0.7665	0.766	0.00542	0.758–0.772	1.453	1.455	0.02132	1.429–1.488

standard deviation.

occurrence of contrasting isotope signatures for different sources of Hg. This idea is negated, however, by the fact that the isotope ratios in the zone of anthropogenic Hg are unrelated to the total Hg concentration and, hence, are independent of variations in the proportion of Hg from local sources of pollution to background Hg from other sources. The fact that the $^{199}Hg/^{201}Hg$ ratio shows little variation within the sediment sequence overlying the basal section of this zone, despite enormous variation in total Hg content due to increases and decreases in the severity of pollution, and is covariant with the Mn/Fe ratio but independent of total Hg concentration, constitutes strong evidence that isotope composition was determined by certain physicochemical and biological processes characteristic of the sedimentary environment and bears no discernible imprint of the original isotope composition of the Hg. The abrupt and drastic change in the behaviour of Hg on going from the background zone to the anthropogenic zone, along with the fact that the isotope ratios consistently conform to the same distinctive pattern of variation throughout the anthropogenic zone (not counting the basal section), despite large variations in the proportion of anthropogenic Hg of local origin to diffuse background Hg, suggests the influence of environmental changes caused by human activities that occurred contemporaneously with Hg pollution and continued over the entire time interval in which the sediments of the anthropogenic zone were laid down. However, some influence of the source of the Hg cannot be ruled out altogether; nor do the data for Lake Ontario preclude the possible existence of source-related isotopic signatures elsewhere.

One possible reason for the inverse correlation of the $^{199}Hg/^{201}Hg$ ratio with the Mn/Fe ratio in the background zone is that the activities of microbes which convert Hg(II) to Hg(0) increased with increasing aeration (Jackson 1998*a*), causing the sediment to be preferentially depleted in the lighter isotope, owing to the escape of isotopically light gaseous Hg(0) into the atmosphere. It is likely, though, that many different isotope-fractionating processes were responsible for the observed overall effect (Rankama 1956, 1963). In the anthropogenic zone, alteration of the environmental regime by pollutants (including pollutants other than Hg) may have brought about a profound change in the nature of the microbial community, leading to an entirely different relationship between Hg isotope fractionation and sediment Eh.

Moving on to other Hg isotope ratios, we find that a plot of the $^{201}Hg/^{204}Hg$ ratio against the Mn/Fe ratio of the $NH_2OH{\cdot}HCl/HNO_3$ extract (Fig. 3; Tables 2 and 3) also resolves itself into a family of significant regression lines: two converging curves representing the peak I (7- to 8-cm to 10- to 11-cm) and peak II (10- to 11-cm to 13- to 14-cm) regions of the background zone, and a separate but roughly parallel curve for the 3- to 4-cm to 6- to 7-cm sections of the anthropogenic zone (the region showing temporal increase in total Hg to a maximum). But in this case, all three of the curves represent positive correlations, and the curve for the anthropogenic zone lies above the two curves for the background zone. Moreover, the 0- to 1-cm to 2- to 3-cm sections of the anthropogenic zone (the region representing pollution abatement) are highly anomalous with respect to the 3- to 4-cm to 6- to 7-cm sections. Another noteworthy feature is that, in Fig. 3 and in the other plots that follow (see below), the lowest anthropogenic horizon (the 6- to 7-cm section) falls in line with the other parts of the 3- to 4-cm to 6- to 7-cm region of the anthropogenic zone. Also note that the trends shown by the $^{201}Hg/^{204}Hg$ ratio (Fig. 3) are essentially the inverse of the trends shown by the $^{199}Hg/^{201}Hg$ ratio (Fig. 2). Probably the reason is that ^{201}Hg is the numerator of the one ratio and the denominator of the other. In other words, the two ratios are not entirely independent of each other and, therefore, display partial self-correlation. Nonetheless, a comparison of Figs. 2 and 3 is instructive, because Fig. 3, unlike Fig. 2, reveals (*i*) a profound difference between the regions of increasing and decreasing pollution in the zone of anthropogenic Hg, (*ii*) essential similarity between all three regression lines, and (*iii*) conformity of the 6- to 7-cm section to the other parts of the region of increasing pollution in the anthropogenic zone. The contrast between the upper and lower regions of the anthropogenic zone suggests an important difference in sedimentary environment, as implied by their radically different Mn/Fe ratios, and, correspondingly, in the nature of the sedimentary microflora. Another point worth mentioning is that, in the 7- to

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Table 3. Solvent extractable Mn and Fe fractions in consecutive 1-cm sections of the core from the Niagara Basin of Lake Ontario.

Depth (cm)	$NH_2OH{\cdot}HCl/HNO_3$-extractable fractions						Citrate/dithionite-extractable Fe ($mg{\cdot}g^{-1}$)		Total extractable Fe ($mg{\cdot}g^{-1}$)	
	Mn ($\mu g{\cdot}g^{-1}$)		Fe ($\mu g{\cdot}g^{-1}$)		Mn/Fe (wt./wt.)					
	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range
0–1	286.425	284.79–288.06	63.12	59.68–66.56	4.550	4.328–4.772	20.14	19.70–20.58	20.309	19.862–20.756
1–2	316.33	315.63–317.03	42.54	38.63–46.45	7.498	6.825–8.171	26.855	22.28–31.43	26.989	22.424–31.555
2–3	276.795	265.62–287.97	33.455	32.53–34.38	8.289	7.726–8.852	22.125	20.46–23.79	22.250	20.579–23.9205
3–4	242.565	241.78–243.35	261.46	244.43–278.49	0.93149	0.87382–0.98916	14.055	13.27–14.84	14.585	13.737–15.434
4–5	228.28	218.59–237.97	354.18	266.44–441.92	0.67945	0.53849–0.82041	16.995	10.58–23.41	18.269	11.849–24.689
5–6	231.445	227.05–235.84	484.99	480.53–489.45	0.47734	0.46389–0.49079	10.28	10.08–10.48	11.916	11.782–12.0495
6–7	243.80	242.32–245.28	612.37	581.58–643.16	0.399015	0.38137–0.41666	7.48	6.91–8.05	8.830	8.230–9.430
7–8	218.735	214.79–222.68	740.45	731.51–749.39	0.295515	0.28662–0.30441	10.925	7.26–14.59	12.483	8.681–16.284
8–9	249.085	242.34–255.83	462.97	348.22–577.72	0.569385	0.44283–0.69594	27.56	25.86–29.26	28.8655	27.083–30.648
9–10	257.58	255.89–259.27	331.47	315.05–347.89	0.77925	0.73555–0.82295	9.965	9.61–10.32	11.044	10.751–11.336
10–11	288.585	288.29–288.88	171.875	117.91–225.84	1.86205	1.2791–2.4450	11.585	11.54–11.63	12.415	12.222–12.608
11–12	306.255	303.64–308.87	455.61	342.50–568.72	0.717855	0.53390–0.90181	34.105	27.44–40.77	35.566	29.093–42.040
12–13	275.00	263.72–286.28	472.515	299.54–645.49	0.682145	0.40856–0.95573	68.74	58.94–78.54	69.909	60.253–79.5645
13–14	272.435	271.34–273.53	217.965	217.73–218.20	1.2499	1.2462–1.2536	16.295	14.94–17.65	16.860	15.556–18.163

Note: "Total extractable Fe" is Fe extracted sequentially with $NH_2OH{\cdot}HCl/HNO_3$, $H_2O_2/NH_4Ac/HNO_3$, and citrate/dithionite. The Fe and Mn concentrations are expressed on the basis of the unit dry weight of the sediment.

8-cm to 10- to 11-cm region of the background zone, the $^{201}Hg/^{204}Hg$ ratio gave a less significant correlation with the Mn/Fe ratio ($P > 0.02$, < 0.05) (Fig. 3) than with Mn alone ($r = 0.992$; $P > 0.001$, < 0.01) or Fe alone ($r = -0.998$; $P > 0.001$, < 0.01), although the opposite is true for the other two regions of the core (the P values for Mn and Fe ranging from >0.02, <0.05 to >>0.1). Nevertheless, only the Mn/Fe ratio gave significant correlation coefficients for all three of the curves in Fig. 3. In any case, the curves in Fig. 3, as with those in Fig. 2, are subject to interpretation in terms of the biogeochemical processes related directly or indirectly to sediment Eh, and different effects were produced in the three regions of the core owing to environmental differences at the time of deposition.

The $^{202}Hg/^{204}Hg$ ratio of the background zone gave an extremely significant positive correlation with the Mn/Fe ratio of the $NH_2OH{\cdot}HCl/HNO_3$ extract and an even stronger inverse correlation with $NH_2OH{\cdot}HCl/HNO_3$-extractable Fe ($P < 0.001$ for both plots) (Fig. 4; Tables 2 and 3), but only a weak correlation with $NH_2OH{\cdot}HCl/HNO_3$-extractable Mn ($r = 0.674$; $P > 0.05$, < 0.1). In Fig. 4, unlike Figs. 2 and 3, all seven sections of the background zone conform to the same trends, and there is remarkably little scatter. In contrast, the isotope ratios of the anthropogenic zone as a whole are virtually independent of the Mn/Fe and Fe data as well as the Mn data (all three P values being >>0.1). The isotope ratios of the 3- to 4-cm to 6- to 7-cm region of the anthropogenic zone lie above the curves for the background zone and tend to parallel them (Fig. 4), but the trend is weak (P ranging from >0.05, <0.1 in Fig. 4*a* to >0.1 in Fig. 4*b*).

Obviously, the strong correlation between the $^{202}H/^{204}Hg$ and Mn/Fe ratios (Fig. 4*a*) is due chiefly to Fe (Fig. 4*b*). Insofar as this particular isotope ratio is concerned, therefore, the relationship between isotope composition and sediment Eh is not as clear-cut as with the $^{199}Hg/^{201}Hg$ ratio. Possibly the $^{202}Hg/^{204}Hg$ ratio was largely determined by some process or complex of processes, or a set of environmental conditions, that was linked directly or indirectly to the precipitation of FeOOH (e.g., certain microbial activities) or to direct interaction between Hg and FeOOH (e.g., preferential sorption of the heavier isotope by FeOOH and preferential desorption of the lighter isotope (Rankama 1956; Hoefs 1973)). Perhaps the most puzzling feature of the $^{202}Hg/^{204}Hg$ data is that the variations of this ratio with respect to Mn, Fe, and the Mn/Fe ratio are so radically different from those of the $^{199}Hg/^{201}Hg$ ratio (in particular, compare Figs. 2 and 4*a*). Intuitively, one would expect the two isotope ratios to yield similar patterns of variation, because each of them represents a lighter isotope of Hg divided by a heavier one, besides which the difference in mass between ^{199}Hg and ^{201}Hg is the same as the difference in mass between ^{202}Hg and ^{204}Hg. In this case, the contrast cannot be explained by the occurrence of a common simple variable in each of the two compound variables, as with the $^{199}Hg/^{201}Hg$ and $^{201}Hg/^{204}Hg$ ratios (see above). Further research is required to explain this mystery. Perhaps it reflects the fact that the fractionation of Hg isotopes in nature is a complex process involving many different reactions occurring simultaneously or in succession at different rates and as functions—possibly nonlinear functions—of many physicochemical and biological factors, all of which are subject to spatial and temporal variation. Under the circum-

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Fig. 2. Variations in the $^{199}Hg/^{201}Hg$ ratio of the sediment as functions of the Mn/Fe ratio of the $NH_2OH{\cdot}HCl/HNO_3$-extractable fraction of the sediment in the zones of anthropogenic and background Hg in the core from the Niagara Basin of Lake Ontario. Symbols: (*i*) zone of anthropogenic Hg: 0- to 1-cm to 2- to 3-cm sections (region of decreasing pollution), □; 3- to 4-cm to 5- to 6-cm sections (region in which pollution is increasing to a maximum, excluding the 6- to 7-cm section), △; 6- to 7-cm section (base of the zone), ▲; (*ii*) zone of background Hg: 7- to 8-cm to 9- to 10-cm sections (peak I region), ●; 10- to 11-cm section (boundary between the peak I and peak II regions), ◆; 11- to 12-cm to 13- to 14-cm sections (peak II region), ■.

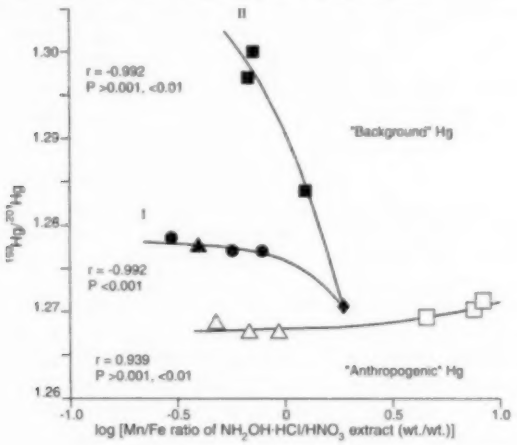


Fig. 3. Variations of the $^{201}Hg/^{204}Hg$ ratio of the sediment as functions of the Mn/Fe ratio of the $NH_2OH{\cdot}HCl/HNO_3$ extract of the sediment in the zones of anthropogenic and background Hg in the core from the Niagara Basin of Lake Ontario. Symbols: (*i*) zone of anthropogenic Hg: 0- to 1-cm to 2- to 3-cm sections (region of decreasing pollution), □; 3- to 4-cm to 6- to 7-cm sections (region in which pollution is increasing to a maximum), △; (*ii*) zone of background Hg: 7- to 8-cm to 9- to 10-cm sections (peak I region), ●; 10- to 11-cm section (boundary between peak I and peak II regions), ◆; 11- to 12-cm to 13- to 14-cm sections (peak II region), ■.

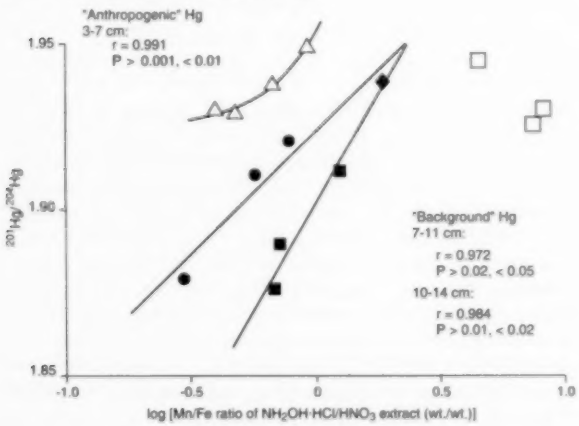
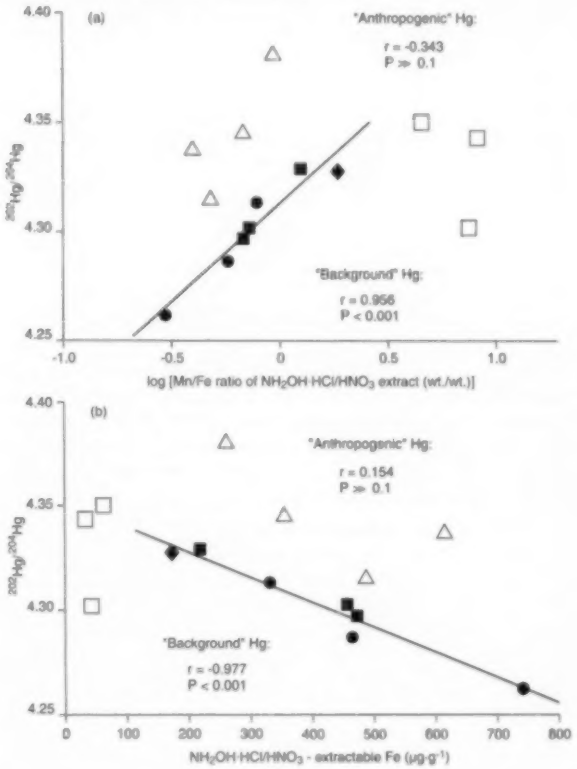


Fig. 4. Variations of the $^{202}Hg/^{204}Hg$ ratio of the sediment with respect to the Mn/Fe ratio of the $NH_2OH{\cdot}HCl/HNO_3$ extract (*a*) and the $NH_2OH{\cdot}HCl/HNO_3$-extractable Fe content (*b*) of the sediment in the Niagara Basin of Lake Ontario. Symbols: (*i*) zone of anthropogenic Hg: 0- to 1-cm to 2- to 3-cm sections (region of decreasing pollution), □; 3- to 4-cm to 6- to 7-cm sections (region in which pollution is increasing to a maximum), △; (*ii*) zone of background Hg: 7- to 8-cm to 9- to 10-cm sections (peak I region), ●; 10- to 11-cm section (boundary between peak I and peak II regions), ◆; 11- to 12-cm to 13- to 14-cm sections (peak II region), ■.



stances, some isotope ratios could conceivably give quite different results than others.

Although the $^{202}Hg/^{204}Hg$ ratio correlates strongly with $NH_2OH{\cdot}HCl/HNO_3$-extractable Fe but weakly with $NH_2OH{\cdot}HCl/HNO_3$-extractable Mn, the opposite is true of the $^{200}Hg/^{202}Hg$ ratio (the ratio of the two most abundant Hg isotopes (Bainbridge and Nier 1950; Rankama 1956)) (Fig. 5; Tables 2 and 3). The $^{200}Hg/^{202}Hg$ ratio gave a significant inverse correlation with $NH_2OH{\cdot}HCl/HNO_3$-extractable Mn ($P > 0.01$, < 0.02) (Fig. 5) but highly insignificant correlations with $NH_2OH{\cdot}HCl/HNO_3$-extractable Fe ($r = 0.381$; $P >> 0.1$) and the Mn/Fe ratio of the $NH_2OH{\cdot}HCl/HNO_3$ extract ($r = -0.518$; $P >> 0.1$). These relationships suggest that the variation in the $^{200}Hg/^{202}Hg$ ratio is linked specifically to the formation of MnOOH, either because both were functions of certain environmental factors and microbial processes or because MnOOH preferentially bound the heavier isotope and released the lighter one (Rankama 1956; Hoefs 1973).

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Fig. 5. Variation of the $^{200}Hg/^{202}Hg$ ratio as a function of the $NH_2OH{\cdot}HCl/HNO_3$-extractable Mn concentration in the zone of background Hg in the sediment core from the Niagara Basin of Lake Ontario. Symbols: 7- to 8-cm to 9- to 10-cm sections (peak I region), ●; 10- to 11-cm section (boundary between peak I and peak II regions), ◆; 11- to 12-cm to 13- to 14-cm sections (peak II region), ■.

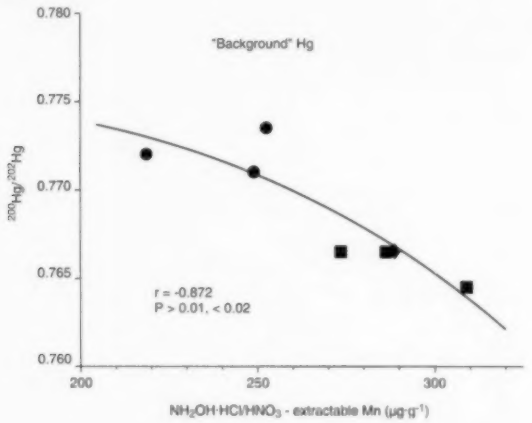
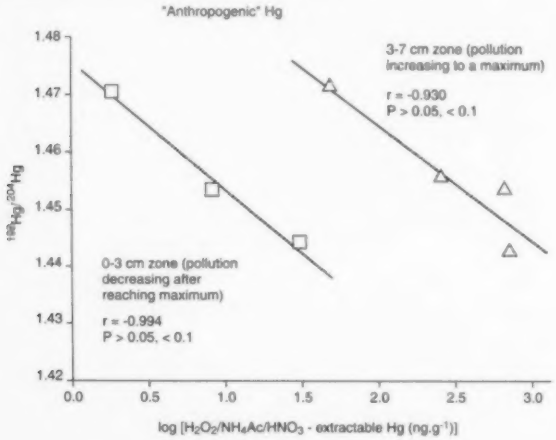


Fig. 6. Variations of the $^{198}Hg/^{204}Hg$ ratio with respect to $H_2O_2/NH_4Ac/HNO_3$-extractable Hg in the zone of anthropogenic Hg in the core from the Niagara Basin of Lake Ontario. Symbols: 0- to 1-cm to 2- to 3-cm sections (region of decreasing pollution), □; 3- to 4-cm to 6- to 7-cm sections (region in which pollution is increasing to a maximum), △.



Nevertheless, the difference between the results for the $^{202}Hg/^{204}Hg$ and $^{200}Hg/^{202}Hg$ ratios is probably due, in part, to the fact that ^{202}Hg is the numerator of the former but the denominator of the latter.

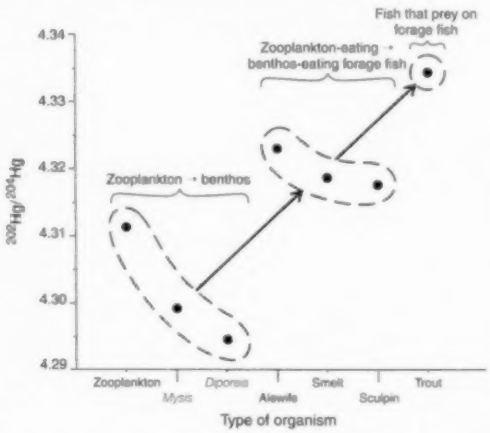
Finally, we come to the $^{198}Hg/^{204}Hg$ ratio, which is of interest because it is the ratio of the lightest isotope (not counting ^{196}Hg) to the heaviest. The results are unlike any of the others. The $^{198}Hg/^{204}Hg$ ratios of the 0- to 1-cm to 2- to 3-cm and 3- to 4-cm to 6- to 7-cm regions of the anthropogenic zone vary inversely with the $H_2O_2/NH_4Ac/HNO_3$-extractable (organically bound) Hg content of the sediment, but the two

Table 4. Concentrations of $H_2O_2/NH_4Ac/HNO_3$-extractable Hg in consecutive 1-cm sections of the core from the Niagara Basin of Lake Ontario.

	$H_2O_2/NH_4Ac/HNO_3$-extractable Hg (ng·g⁻¹)	
Depth (cm)	Mean	Range
0–1	1.845	1.56–2.13
1–2	8.265	8.26–8.27
2–3	30.85	27.60–34.10
3–4	670.91	666.03–675.79
4–5	716.925	693.46–740.39
5–6	257.14	253.59–260.69
6–7	49.05	46.15–51.95
7–8	20.265	18.63–21.90
8–9	15.115	14.59–15.64
9–10	13.375	12.16–14.59
10–11	12.32	11.55–13.09
11–12	18.05	17.00–19.10
12–13	13.695	12.28–15.11
13–14	13.65	13.57–13.73

Note: The Hg concentrations are based on the unit dry weight of the sediment.

Fig. 7. Variations in the $^{202}Hg/^{204}Hg$ ratios of food-web animals from the Niagara Basin of Lake Ontario. Organisms at the same trophic level are represented by points surrounded by a dashed line, and the large arrows point from lower to higher trophic levels.



regions show separate, though nearly parallel, trends covering different ranges of $H_2O_2/NH_4Ac/HNO_3$-extractable Hg concentrations (Fig. 6; Tables 2 and 4). Although the correlations are not very strong ($P > 0.05, < 0.1$), the regularity of the two trends and their similarity to each other suggest that the relationships are real. The sharp separation of the curves constitutes further evidence that the two regions of the anthropogenic zone represent different environmental conditions and, hence, different isotope-fractionating effects. Isotope fractionation could have resulted from preferential binding of the heavier isotope and release of the lighter one by organic matter (Rankama 1956; Hoefs 1973). The $^{198}Hg/^{204}Hg$ ratios of the background Hg zone, however, vary independently of $H_2O_2/NH_4Ac/HNO_3$-extractable Hg ($r = -0.205$; $P >> 0.1$), possibly because the background Hg was associ-

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Table 5. The $^{202}Hg/^{204}Hg$, $^{199}Hg/^{204}Hg$, $^{198}Hg/^{199}Hg$, $^{201}Hg/^{204}Hg$, $^{198}Hg/^{204}Hg$, and $^{200}Hg/^{202}Hg$ ratios of the food-web animals from the Niagara Basin of Lake Ontario. (Table 5 is concluded on pages 194 and 195.)

		$^{202}Hg/^{204}Hg$				$^{199}Hg/^{204}Hg$			
Type of organism	*N*	Median	Mean	SD	Range	Median	Mean	SD	Range
Zooplankton (mostly cladocerans)	2	4.311	4.311	0.02760	4.292–4.331	2.430	2.430	0.01980	2.416–2.444
Mysis relicta	2	4.299	4.299	0.005228	4.296–4.303	2.427	2.427	0.005657	2.423–2.431
Diporeia hoyi	2	4.295	4.295	0.01435	4.284–4.305	2.4255	2.4255	0.01061	2.418–2.433
Alewife (*Alosa pseudoharengus*)	4	4.326	4.323	0.01277	4.305–4.335	2.442	2.441	0.008869	2.430–2.450
Rainbow smelt (*Osmerus mordax*)	4	4.322	4.319	0.01532	4.299–4.333	2.442	2.440	0.01103	2.425–2.450
Slimy sculpin (*Cottus cognatus*)	4	4.320	4.318	0.009372	4.305–4.327	2.445	2.442	0.008717	2.434–2.450
Lake trout (*Salvelinus namaycush*)	4	4.337	4.335	0.01201	4.320–4.348	2.451	2.4505	0.005508	2.444–2.456

Note: *N* is the number of replicate analyses (= two for single samples analysed in duplicate and four for duplicate samples analysed in duplicate); SD is the standard deviation.

ated mainly with oxyhydroxides rather than with organic matter.

The food-web animals

Among the biological specimens, the $^{202}Hg/^{204}Hg$ ratio varies systematically with respect to trophic level, habitat, and diet (Fig. 7; Table 5), and the data for the Hg standard solution fluctuate randomly about a vertical line, demonstrating the absence of bogus trends due to systematic drift in the readings during analysis (T.A. Jackson, unpublished data). The $^{199}Hg/^{204}Hg$, $^{201}Hg/^{204}Hg$, $^{198}Hg/^{199}Hg$, $^{198}Hg/^{204}Hg$, and $^{200}Hg/^{202}Hg$ ratios (Table 5) show weaker, less-consistent relationships with trophic level and the other biological factors, and the $^{199}Hg/^{201}Hg$ ratio (T.A. Jackson, unpublished data) shows no apparent relationship at all.

The $^{202}Hg/^{204}Hg$ ratio increases progressively from lower to higher trophic levels, i.e., in the sequence crustaceans < forage fish < lake trout (*Salvelinus namaycush*). But superimposed on this trend are two secondary trends parallel to each other, one for the crustaceans and the other for the forage fish. Among the crustaceans, the isotope ratio *decreases* in the order zooplankton (a 153 μm net sample composed mostly of cladocerans) > *Mysis relicta* (a mysid that is both planktonic and benthic) > *Diporeia hoyi* (a benthic amphipod). This sequence demonstrates that Hg in planktonic crustaceans tends to be isotopically lighter than Hg in benthic ones; the tendency is especially convincing, because the $^{202}Hg/^{204}Hg$ ratio of *M. relicta*, which is both planktonic and benthic, is intermediate between the $^{202}Hg/^{204}Hg$ ratios of the purely planktonic and purely benthic species. Among forage fish, the $^{202}Hg/^{204}Hg$ ratio decreases in the order alewife (*Alosa pseudoharengus*) > rainbow smelt (*Osmerus mordax*) > slimy sculpin (*Cottus cognatus*). This trend corresponds perfectly to the trend observed in the crustaceans on which the fish feed: Alewife eat comparable amounts of zooplankton and *Mysis* (with minor quantities of *Diporeia*), smelt feed mainly on *Mysis* (with smaller amounts of *Diporeia*), and sculpin feed primarily on *Diporeia* (with smaller amounts of *Mysis*). Thus, the variation in Hg isotope composition seen in the fish reflects the feeding habits of the fish. Evidently the isotope composition of a forage fish is determined largely by the isotope composition of its food, resulting in modification of the overall tendency toward higher isotope ratios at higher trophic levels. This conclusion is consistent with radioactive-tracer data indicating that, in slimy sculpin and lake trout at least, direct absorption of Hg from water is not a major pathway of Hg uptake, implying that food is the principal vehicle for uptake (Klaverkamp et al. 1983; Harrison et al. 1990). The importance of dietary sources of Hg is widely recognised (Spry and Wiener 1991; Rodgers 1994).

Although more research is needed to explain these results, all available information supports the hypothesis that the $^{202}Hg/^{204}Hg$ ratios of the animals increase with the proportion of CH_3Hg^+ to unmethylated Hg in their tissues, suggesting that CH_3Hg^+ tends to have a higher $^{202}Hg/^{204}Hg$ ratio than the inorganic Hg(II) from which it is formed. This inference is based on the well-established fact that concentrations of CH_3Hg^+ (but not inorganic Hg(II)) in aquatic organisms generally increase from lower to higher trophic levels (Jackson 1991, 1998*a*; Spry and Wiener 1991) and on indirect evidence that plankton and plankton-eating fish have higher proportions of CH_3Hg^+ to unmethylated Hg than benthic invertebrates and benthos-eating fish, respectively, in at least some cases (Jackson 1991). The specimens were not analysed for CH_3Hg^+, but their total Hg content is consistent with the author's interpretation, as it is highest at the highest trophic level, where we would expect to find the greatest abundance of Hg, most of it in the form of CH_3Hg^+. Thus, the mean Hg content of lake trout was 175 $ng \cdot g^{-1}$ wet weight (with a range of 146–197 $ng \cdot g^{-1}$), whereas the Hg levels in the other organisms were mostly on the order of several tens of nanograms per gram (with a total range of 3–139 $ng \cdot g^{-1}$). It seems likely, then, that the fractionation of Hg isotopes occurred during microbial methylation of Hg in the environment, although other factors, such as the preferential release of isotopically lighter CH_3Hg^+ molecules from sediments into the overlying water and the preferential uptake of isotopically lighter CH_3Hg^+ by the organisms, could have been involved.

Another observation worth noting is that the $^{202}Hg/^{204}Hg$ ratio of the surface sediment, as represented by the 0- to 1-cm section of the core (4.350) (Table 2), is higher than the $^{202}Hg/^{204}Hg$ ratios of the biota (4.295–4.335) (Table 5). The mean value for the 0- to 3-cm region of the core is 4.330, which is slightly lower than the value for lake trout (4.335) but higher than any of the values for the other animals (which fall in the range 4.295–4.323). The mean ratio value for a depth of 0–5 cm is 4.344 and the mean value for a depth of 0–7 cm (i.e., the entire zone of anthropogenic Hg) is 4.340; both of these values are higher than the value for lake trout. In brief, the Hg-polluted upper horizons of the sediment

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Table 5 (*concluded*).

Type of organism	$^{198}Hg/^{199}Hg$				$^{201}Hg/^{204}Hg$			
	Median	Mean	SD	Range	Median	Mean	SD	Range
Zooplankton (mostly cladocerans)	0.5962	0.5962	0.005515	0.5923–0.6001	1.904	1.904	0.01980	1.890–1.918
Mysis relicta	0.59825	0.59825	0.001061	0.5975–0.5990	1.898	1.898	0.001414	1.897–1.899
Diporeia hoyi	0.5969	0.5969	0.003536	0.5944–0.5994	1.901	1.901	0.001414	1.900–1.902
Alewife (*Alosa pseudoharengus*)	0.5929	0.5929	0.001098	0.5919–0.5939	1.9125	1.911	0.004349	1.905–1.915
Rainbow smelt (*Osmerus mordax*)	0.59615	0.5959	0.003255	0.5920–0.5994	1.9125	1.9115	0.006245	1.903–1.918
Slimy sculpin (*Cottus cognatus*)	0.5935	0.59335	0.001328	0.5918–0.5946	1.908	1.909	0.004646	1.904–1.915
Lake trout (*Salvelinus namaycush*)	0.59285	0.5929	0.001928	0.5910–0.5950	1.919	1.9195	0.007767	1.911–1.929

have isotopically lighter Hg than the food-web animals, insofar as the $^{202}Hg/^{204}Hg$ ratio is concerned. These results suggest that the processes responsible for the Hg isotope fractionation seen in food-web organisms differ appreciably from the isotope-fractionating processes that prevail in the associated sediments. Further work, of course, is needed to explain why the $^{202}Hg/^{204}Hg$ ratio showed more pronounced and consistent correlations with trophic level and other biological factors than the other isotope ratios did. As with the sediment data, a possible reason is that Hg isotope fractionation is a complex process involving many individual reactions and is controlled by a number of different environmental and biological factors, the observed result being the net effect of all these diverse phenomena. The kinetics of the reactions could be appreciably different for different isotopes of Hg, resulting in the observed difference in the relationships between Hg isotope ratios and biological factors such as trophic level, habitat, and diet.

The cinnabar reference sample

Statistical data for the $^{199}Hg/^{201}Hg$, $^{202}Hg/^{204}Hg$, $^{198}Hg/^{204}Hg$, and $^{200}Hg/^{202}Hg$ ratios of the cinnabar sample from the Almaden Hg mine are shown in Table 6. Comparison with the equivalent results for the core sections (Table 2) and biological specimens (Table 5) revealed systematic differences. For the most part, the cinnabar was isotopically lighter than the sediments and organisms. Thus, the $^{199}Hg/^{201}Hg$, $^{202}Hg/^{204}Hg$, $^{198}Hg/^{204}Hg$, and $^{200}Hg/^{202}Hg$ ratios are higher in the cinnabar than in most of the core sections. Insofar as the $^{202}Hg/^{204}Hg$ and $^{198}Hg/^{204}Hg$ ratios are concerned, the cinnabar is isotopically lighter than any of the organisms, although the $^{200}Hg/^{202}Hg$ ratios for the organisms are mostly similar to the value for cinnabar and seem not to differ systematically from it.

The systematic differences in Hg isotope composition between the cinnabar sample and the core sections and biological specimens are further indications that fractionation of Hg isotopes occurs in nature. The fact that the cinnabar shows the same general tendency with respect to two such unlike materials as the sediments and biota, which tend to differ from each other in isotope composition, suggests that the formation of the cinnabar involved appreciable separation of Hg isotopes. This hypothesis is consistent with both the general theory of isotope fractionation and the results of experimental separation of Hg isotopes (see Introduction). As the cinnabar precipitated from hydrothermal solutions of relatively low temperature migrating upward through the Earth's crust from a body of magma below the surface (Bateman 1950), there could well have been a tendency toward preferential movement of the lighter isotopes, resulting in concentration of these isotopes in the precipitate. The comparatively low temperatures of the hydrothermal solutions make isotope separation during migration of the Hg from its source to the site of deposition in the host rock all the more likely (Hoefs 1973).

The standard deviations for all four of the isotope ratios of the cinnabar fall within the range of standard deviations for the Lake Ontario core samples (Table 2), indicating a comparable degree of dispersion, even though fewer replicate analyses were done in the case of the core sections. However, there is some ambiguity here, because the standard deviations for the core tend to be higher in the zone of background Hg than in the zone of anthropogenic Hg, as might have been predicted from the fact that the total Hg levels are lower in the background zone: Presumably the random analytical error was greatest where the Hg content was lowest. Perhaps it would be more meaningful to say that the standard deviations for the cinnabar specimen are comparable with the low to intermediate standard deviations of the core sections.

One peculiarity of the standard deviations that is immediately apparent from inspection is that the values for the $^{202}Hg/^{204}Hg$ ratios of both the cinnabar and the core sections are aberrantly high with respect to the standard deviations of the other isotope ratios of these materials (Tables 2 and 6). Possibly the abnormally high degree of scatter implied by the data for this ratio is related to the fact that ^{202}Hg and ^{204}Hg are the most abundant and least abundant isotopes, respectively (Bainbridge and Nier 1950; Rankama 1956). The observation that anomalously high standard deviations are characteristic of this particular isotope ratio, irrespective of whether the sample material is cinnabar or sediment and despite homogenisation of the samples prior to analysis, is consistent with the possibility that the high values are artifacts of the analytical technique rather than peculiarities of the samples. Yet this interpretation would seem to be incompatible with the fact that the plots of the median $^{202}Hg/^{204}Hg$ values for the core sections against the Mn/Fe ratio of the $NH_2OH{\cdot}HCl/HNO_3$ extract and the concentration of $NH_2OH{\cdot}HCl/HNO_3$-extractable Fe gave highly significant trends with very little scatter (Fig. 4). More research is needed to explain this apparent inconsistency.

As with the core sections, the standard deviations of the $^{198}Hg/^{204}Hg$ and $^{200}Hg/^{202}Hg$ ratios of the cinnabar (Table 6) fall within the ranges of corresponding values for the biological specimens (Table 5). The standard deviations for the $^{200}Hg/^{202}Hg$ ratio, however, are anomalous, as the value for cinnabar is higher than the values for any of the organisms

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$^{198}Hg/^{204}Hg$				$^{200}Hg/^{202}Hg$			
Median	Mean	SD	Range	Median	Mean	SD	Range
1.4485	1.4485	0.002121	1.447–1.450	0.7782	0.7782	0.0009899	0.7775–0.7789
1.4525	1.4525	0.0007071	1.452–1.453	0.77875	0.77875	0.001626	0.7776–0.7799
1.4475	1.4475	0.01485	1.437–1.458	0.7761	0.7761	0.001556	0.7750–0.7772
1.447	1.447	0.004425	1.443–1.452	0.77855	0.7779	0.001578	0.7756–0.7790
1.454	1.454	0.002449	1.451–1.457	0.77785	0.7780	0.001124	0.7769–0.7793
1.4485	1.450	0.004967	1.446–1.457	0.77715	0.7773	0.001682	0.7757–0.7791
1.4535	1.453	0.007616	1.445–1.460	0.77505	0.7745	0.004957	0.7680–0.7800

Table 6. Values of the statistical parameters for Hg isotope data obtained by analysis of 10 replicate portions of a cinnabar sample from the Almaden mercury mine, Spain.

Parameter	$^{199}Hg/^{201}Hg$	$^{202}Hg/^{204}Hg$	$^{198}Hg/^{204}Hg$	$^{200}Hg/^{202}Hg$
Mean	1.284	4.352	1.4645	0.7772
Median	1.286	4.361	1.4625	0.7781
SD	0.007009	0.03800	0.007337	0.003540
SEM	0.002216	0.01202	0.002320	0.001119
Range	1.268–1.292	4.263–4.392	1.455–1.478	0.7703–0.7816

Note: SD is the standard deviation; SEM is the standard error of the mean.

except lake trout (Tables 5 and 6). But the most extreme and intriguing anomaly emerged from the data for the $^{202}Hg/^{204}Hg$ ratio. In this case, the standard deviation for the cinnabar (0.03800) is higher than the standard deviations of any of the food-web animals (0.005228–0.02760) (Tables 5 and 6), even though the number of replicate analyses of the organisms was smaller than those of the cinnabar and despite homogenisation of the samples prior to analysis. By the same token, the range of values for the $^{202}Hg/^{204}Hg$ ratio (the highest value minus the lowest) was much higher for the cinnabar (0.129) than for any of the organisms (0.007–0.039). Moreover, the standard deviations of the $^{202}Hg/^{204}Hg$ ratios of the core sections tend to be higher than those of the organisms, although the ranges of the two sets of measurements overlap (Tables 2 and 5). In short, the $^{202}Hg/^{204}Hg$ ratios show much less random variation in the organisms than in the sediments and, in particular, than in the cinnabar. The uniqueness of the biological data in this regard suggests that the processes responsible for the discrimination between different Hg isotopes by the organisms are characterised by a higher degree of efficiency, selectivity, and consistency than the processes that determined the isotope composition of the sediments and cinnabar.

Summary of results, inferences, and implications, with suggestions for future research

Briefly, the principal results and interpretations are as follows. (*i*) The stable-isotope ratios of Hg in the sediment sequence varied with the Mn and Fe oxyhydroxide content of the sediments and the Mn/Fe ratio of the oxyhydroxide fraction. These systematic variations are attributable to isotope fractionation in the environment, and the processes responsible for the observed effects were probably linked to the Eh of the sediment at the time of deposition. The data showed major fundamental differences between the zone of recent pollution and the underlying older zone of background Hg (and between different regions within each zone), probably owing to differences in sedimentary environment and microbial activities. The results provide no evidence that the Hg from the sources of recent pollution is characterised by a specific isotopic signature. However, this does not rule out the possibility of discovering source-related isotopic signatures, as well as quite different environmental and biologically mediated effects, elsewhere. (Note that preliminary investigation of a core from a small lake contaminated with Hg from a nearby smelter revealed Hg isotope variations that differ radically from the variations observed in the Lake Ontario core (Jackson 1999).) (*ii*) The isotope composition of Hg in food-web animals varied progressively from lower to higher trophic levels, and also from planktonic to benthic crustaceans and, correspondingly, from zooplankton-eating to benthos-eating fish, probably reflecting variations in the abundance of CH_3Hg^+ in relation to unmethylated Hg. (*iii*) The reference specimen of cinnabar showed a marked tendency to be isotopically lighter than the sediments and biota, providing further evidence of Hg isotope fractionation in nature.

These findings imply that systematic variations in the stable-isotope composition of Hg in the environment may provide an as yet untapped and previously unsuspected supply of valuable information about the sources and biogeochemical cycling of natural and anthropogenic Hg. Further research is needed, however, to confirm, extend, and explain the results. More precise and sensitive methods of mass spectrometry (e.g., multicollector ICP-MS) should be used in any future work, and an effort should be made to detect and eliminate possible artifacts, such as false results arising from inadvertent fractionation of Hg isotopes during the extraction and analysis of samples. Sediments representing different environments and different pollution histories, along with a wider variety of organisms, should be compared, and data for field samples should be compared with results of relevant controlled experiments on the fractionation of Hg isotopes by abiotic and biological processes in model environments. One very useful approach would be to compare samples collected along environmental gradients and at different distances from sources of contamination. Another would be to compare data

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for Hg from different sources and from different *kinds* of sources.

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Competition among juvenile Atlantic salmon (*Salmo salar*) and steelhead (*Oncorhynchus mykiss*): relevance to invasion potential in British Columbia

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Abstract: Atlantic salmon (*Salmo salar*) are routinely captured in both freshwater and marine environments of coastal British Columbia (Canada). Recent evidence suggests that this species is now naturally reproducing in Vancouver Island rivers. Our objective was to quantify the performance of each species in intra- and inter-specific competition by assessing the competitive ability of Atlantic salmon sympatric with native niche equivalent steelhead – rainbow trout (*Oncorhynchus mykiss*). Significant behavioural differences, particularly with respect to agonism, were observed between species; however, the status of an individual as resident or challenger was the best predictor of performance. Resident fish always outperformed challengers, regardless of species. Thus, we suggest that Atlantic salmon may be capable of colonizing and persisting in coastal British Columbia river systems that are underutilized by native species, such as the steelhead.

Résumé : On capture couramment des saumons atlantiques (*Salmo salar*) dans des milieux marins ou dulcicoles du littoral de la Colombie-Britannique (Canada). Des données récentes permettent de penser que cette espèce se reproduit maintenant de façon naturelle dans les cours d'eau de l'île de Vancouver. Notre objectif était de quantifier la performance de chaque espèce dans la concurrence intra- et interspécifique en évaluant l'aptitude concurrentielle des saumons atlantiques sympatriques du saumon arc-en-ciel (*Oncorhynchus mykiss*) indigène, dont la niche est équivalente. Des différences de comportement significatives ont été notées, particulièrement sur le plan de l'agonisme, mais c'est le statut d'un individude résident ou de challengeur qui constituait le meilleur prédicteur de la performance. Les poisson résidents dépassaient toujours les challengeurs, quelle que soit l'espèce. Nous jugeons donc que le saumon atlantique est en mesure de coloniser et d'occuper de façon permanente les systèmes côtiers de Colombie-Britannique sous-utilisés par les espèces indigènes comme le saumon arc-en-ciel.

[Traduit par la Rédaction]

Introduction

Aquaculture produces the most valuable export crop in British Columbia, namely, farmed salmon, and approximately 80% of production is Atlantic salmon (*Salmo salar*). Pacific coast aquaculturalists prefer Atlantic salmon, owing to a consistently better market price and its superior performance under culture compared with native species (Keller and Leslie 1996). The balance of production is made up of chinook (*Oncorhynchus tshawytscha*) and coho (*Oncorhynchus kisutch*) salmon. Atlantic salmon are raised in freshwater hatcheries to smolts and then transferred to marine net pens, where they remain and grow to market size. The majority of marine net pen facilities in British Columbia are located off the northeast and west coasts of Vancouver Island. The first capture of a free-ranging Atlantic salmon in British Columbian waters occurred in 1987, and adults are now routinely encountered during the marine commercial salmon season and are also seen in many Vancouver Island rivers from summer through winter each year (McKinnell et al. 1997; Thomson and Candy 1998). In August 1998, the first naturally reproduced Atlantic salmon were captured in the Tsitika River on the northeast coast of Vancouver Island (Volpe et al. 2000). The 12 fish sampled represent the first documented evidence of successful feral spawnings (2 year-classes captured) of aquaculture-escaped Atlantic salmon in British Columbia.

As reports of free-ranging Atlantic salmon become commonplace, and particularly since the discovery of the Tsitika River juveniles, the potential for naturalization of Atlantic salmon in British Columbia has become a contentious issue. Previous failed introductions in British Columbia and elsewhere have been cited as evidence that current aquaculture escapees pose little ecological threat (Needham 1995). Atlantic salmon were introduced to British Columbia early last century but, despite considerable effort, all attempts failed to establish a self-sustaining population (Carl and Guiguet 1958).

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Table 1. Starting densities, weights, and lengths of fish in the three replicate experiments are listed, with the time frame and temperature profile for each replicate.

	Experimental block		
	1	2	3
No. of fish in low-density channels	4	4	2
No. of fish in mixed and high-density channels	8	8	4
No. of fish of each species in mixed channels	4	4	2
Mean start weight of steelhead (g)	0.55	1.09	1.14
Mean start weight of Atlantic salmon (g)	0.55	1.05	1.63
Mean start length of steelhead (mm)	38.7	49.3	47.1
Mean start length of Atlantic salmon (mm)	37.1	48.7	54.3
Residents introduced to channel	22 June	15 June	31 July
Challengers introduced to channel	25 June	18 July	3 August
Experiment ends	6 July	29 July	14 August
Temperature (°C)			
Mean	17.0	18.2	18.5
Range	15.1–17.9	15.0–19.1	16.3–19.1

The cause(s) of these failed introductions remains unknown. Regardless, aquaculture-escapee salmon encounter different biological and physical parameters today than those released earlier this century. As such, it is important to determine colonization potential and future downstream effects of contemporary escapes in a scientific manner.

Juvenile steelhead – rainbow trout (*Oncorhynchus mykiss*) display significant niche overlap with Atlantic salmon and, under limiting circumstances, are likely to come into vigorous competition for resources (Gibson 1981; Hearn and Kynard 1986). We assumed that, if the presence of Atlantic salmon was to affect native populations, the effect would be first and perhaps most vigorously manifested in, although not necessarily restricted to, sympatric steelhead. Our objective was to quantify the performance of each species in intra- and inter-specific competition by assessing the competitive ability of Atlantic salmon sympatric with native niche equivalent steelhead.

Methods

Fish

All experiments were conducted using a single cohort of young-of-the-year fish of each species. We collected progeny of Vancouver Island aquaculture broodstock (McConnel strain) Atlantic salmon from a local commercial aquaculture facility. Fish were reared to emergence and, at 119 days post-hatch (2 June 1998), were haphazardly sampled from pooled spawnings (three females, six males) and moved to the University of Victoria's Aquatic Facility (UVicAF), where they were held under aquaculture-like conditions until required. Steelhead were F_1 progeny of wild adults (three females, six males) taken from the Salmon River, Vancouver Island. Fish were maintained at the Vancouver Island Trout Hatchery (Duncan, B.C.) until transported to UVicAF at 38 days post hatch (also 2 June 1998). Animals were chosen haphazardly from rearing tanks containing mixed pools of progeny.

Fish were held in standard 410-L circular rearing tanks for 20 days prior to the start of the first experiment. The steelhead holding tank was augmented with structural diversity, including cobble substrate and artificial structure, to simulate a more natural environment. While in the holding tanks, steelhead were fed a "high forage rate" (see below) mixture of chironomid larvae and *Daphnia*, the same forage they would encounter in the experimental channels. Atlantic salmon were maintained in an aquaculture-like environment (bare tank) and fed commercial pellet food to satiation. The outdoor holding tanks were equipped with opaque lids, so fish were exposed to natural photoperiod. Temperature in the tanks varied between 15 and 19°C over the course of the experiments, which ran from 22 June to 14 August 1998 (Table 1).

Experimental procedure

A primary objective was to quantify the strength of intraspecific and interspecific competition of sympatric juvenile Atlantic salmon and steelhead. The per capita effect of steelhead on themselves (intraspecific competition or a_{ss}) was measured as the reduction in performance (weight loss) between steelhead at high density and steelhead at low density. The effect of Atlantic salmon on steelhead (interspecific competition or a_{as}) was defined as the change in performance between steelhead sympatric with Atlantic salmon at high density and steelhead alone at low density. Per capita coefficients of intra- and inter-specific competition for Atlantic salmon (a_{aa} and a_{sa}, respectively) were calculated in a similar fashion. Analyses of intra- and inter-specific competition often yield confounded data (Underwood 1986 and references therein; Fausch 1997) as a result of not adequately separating intraspecific from interspecific effects. Because the low-density, high-density, and mixed channels had n, $2n$, and n of steelhead and (or) Atlantic salmon, we could unambiguously separate intraspecific from interspecific effects. Thus, six combinations of fish were used: conspecific Atlantic salmon at low and high density; steelhead at low and high density; and two mixed-species channels, both at high density. These six combinations were each replicated at high and low forage levels, bringing the total number of channels to 12 for the full design. The design was replicated three times as time blocks (see Table 1). Steelhead and Atlantic salmon began the first two replicates at a similar mean size; however, by experiment (time replicate) 3, Atlantic salmon were much heavier than steelhead (Table 1). This was due to the more rapid relative growth of Atlantic salmon in the holding tanks. Both species grew over the course of the experiments and, to compensate, densities had to be halved during replication three (Table 1).

In each of the 12 experimental channels, fish were subjected to a combination of four treatments: (1) species composition (intra- or inter-specific), (2) order of introduction (resident or challenger), (3) fish density (high or low), and (4) forage abundance (high or low) (Fig. 1). For the high-density and mixed channels, four resident fish were acclimatized to the channels for 3 days prior to the introduction of four challenger fish. For the low-density channels, four fish were added at once. Observations began immediately after the introduction of the challengers and continued for 10 days.

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Fig. 1. Schematic representation of the experimental design for one full experiment. Two replicates of six channels were used in each of three experiments: one replicate provided with a high forage level and the other with a low forage level. By comparing results from appropriate channels, intraspecific (a_{ss}, a_{aa}) and interspecific (a_{sa}, a_{as}) competition can be evaluated, as well as the role of residency (assembly). The relevant comparisons are illustrated by brackets between the experimental populations being compared. Within each channel, the number and species of fish (AS, Atlantic salmon; ST, steelhead) are given. The top set indicates the initial fish introduced into the channels, i.e., the *residents*. After a 72-h acclimatization, the fish indicated by the bottom set were introduced, i.e., the *challengers*. Note that both the high-density single- and mixed-species channels had residents and challengers, while low-density single-species channels had only residents.

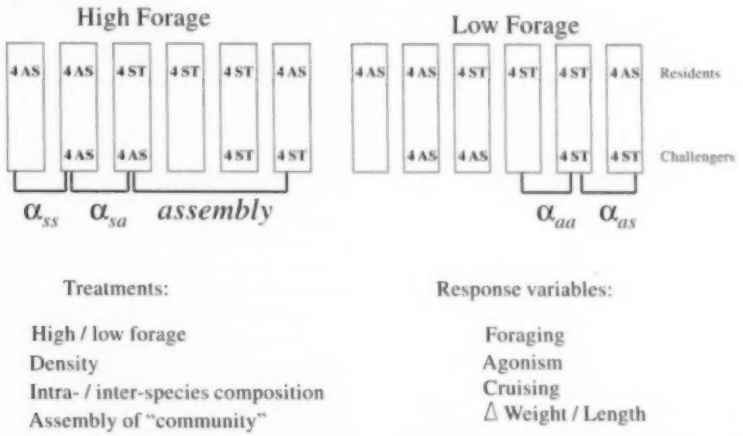
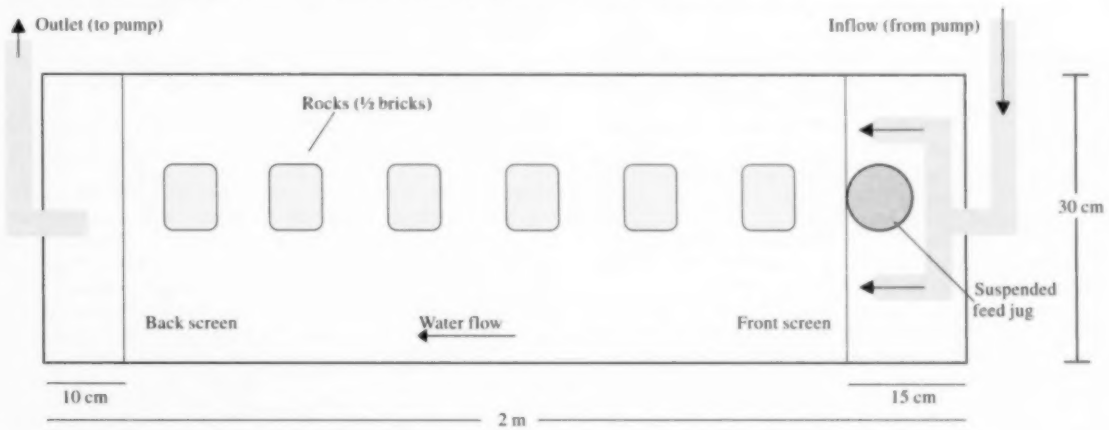


Fig. 2. Schematic representation of a single experimental channel viewed from above. Water entered from a single inlet behind a mesh partition that fish could not pass but which allowed free passage of forage items. Six identical half-bricks provided the only structure in the channel (all channels had the same number of bricks, regardless of composition or density). Water was removed via dual gravity-driven outlets. Ball valves on both the inlet and outlet allowed precise control of flow rates.



Prior to each experiment, fish haphazardly selected from the holding tanks were starved for 12 h to clear the gut, anesthetized with clove oil (Keene et al. 1998), measured (fork length), weighed, and randomly assigned an identifying fin clip. After being measured and weighed, fish were graded, to minimize size differences, and added to randomly chosen channels as residents. By the third replicate, the size difference between species was too great to effectively control for size (Table 1). After a 72-h acclimatization period, during which the resident fish were provided with half the experimental forage level, similarly treated challengers were added to the channels and the forage levels increased to full ration. We used fin notches ("V"-shaped clips) to identify individuals at the beginning and end of each experiment (notches could not be distinguished by observers when fish were in the channels). Some individuals had no notches, while others had notches on one or two of the following fins: adipose, right or left ventral, upper or lower tips of the caudal. Because the duration of each experiment was only 13 days, the regeneration of the clips was not an issue, allowing us to remove only a very small portion of tissue while maintaining individual discrimination.

Food consisted of equal parts frozen adult *Daphnia* spp. and chironomid larvae. Daily rations provided the caloric equivalent of a commercially prepared diet at high and low forage levels (based on standard feeding protocols prepared by EWOS Inc.). Food was dispensed via an inverted 4-L plastic jug suspended above each channel upstream of the top fence (Fig. 2). The jugs were partially filled with shaved ice and the appropriate ration for 1 day, shaken to distribute the forage items, and then filled with dechlorinated filtered water and frozen solid overnight. When frozen, the forage items were randomly distributed throughout the jug, which re-

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Table 2. Main response variables per 5-min observation, together with total sampling effort.

	Experimental block			
	1	2	3	Mean
Δweight (g)				
Steelhead	0.00	−1.03	0.00	−0.34
Atlantic salmon	−0.04	−0.14	−0.08	−0.09
Δlength (mm)				
Steelhead	0.90	0.00	1.43	0.78
Atlantic salmon	1.30	0.61	1.12	1.01
Counts/5 min				
Intraspecific agonism				
Steelhead	1.40	2.15	0.72	1.42
Atlantic salmon	0.22	0.19	0.20	0.20
Interspecific agonism				
Steelhead	0.51	0.56	0.34	0.47
Atlantic salmon	0.11	0.15	0.27	0.18
Forage				
Steelhead	5.92	2.23	1.61	3.25
Atlantic salmon	4.91	2.51	1.35	2.92
Cruise				
Steelhead	5.60	7.82	8.03	7.15
Atlantic salmon	1.43	1.28	2.04	1.58
Total no. of 5-min observations				
Steelhead	127	128	104	na
Atlantic salmon	82	130	110	na

Note: Values for each variable are adjusted for sampling effort and represent the total number of observations across all treatments. Agonism values are means across all treatments. Interspecific-agonism values are adjusted to account for the different number of conspecific and interspecific individuals available for interaction relative to the focal individual.

quired approximately 24–26 h to thaw completely. A hole punched in the lid of each jug allowed the thawing water and forage to drip into the channel. Forage entered the channel unpredictably over the thawing period. Freshly prepared jugs were provided when the previous day's jug was completely empty.

Both species showed normal feeding behaviour upon entering the channels. Even though Atlantic salmon had not encountered natural drifting forage before entering the channels, we did not note any delay in acceptance of drift forage. Both species fed exclusively on moving drift, ignoring any forage item that came to rest on the substrate or on the front and rear fences.

Experimental channels were 2.0 m long, 0.3 m wide, and 8 cm deep. Natural light and photoperiod were provided by overhead skylight windows. All channels were surrounded by opaque black fabric, to minimize disturbance. Six cement bricks (6 × 6 × 3.5 cm) treated with a biologically inert sealer (Thompson's Water Seal®) were placed in each channel, to serve as current refuges, and were the only structures in the channels (Fig. 2). All bricks were identical, to ensure that any observed territoriality was a function of the brick position in the channel and not of the brick itself. A single layer of river cobble (2–3 cm in diameter) covered the remainder of the bottom of each arena. Victoria municipal water that had been dechlorinated with thiosulphate was provided in a partial-recirculation system (15% replacement per cycle), at a rate of 40 $L \cdot min^{-1}$, providing a maximum surface velocity of 0.25 $m \cdot s^{-1}$. Water temperature varied from 15 to 19°C over the course of the experiment. Water chemistry was maintained by passing water through a series of sand filters, charcoal beds, a biofilter, and an aeration tower every cycle.

Experimental stocking density was determined in a pilot experiment using steelhead. Two raceways were stocked to what was considered excess (15 steelhead). Each channel allowed emigration through a one-way trap to a refuge, an adjacent suboptimal channel with minimal flow and no food. Fish in the primary channel experienced natural photoperiod and a high-ration diet. After 48 h, relative positions and densities of fish were assessed for 15 min every 3 h (Hearn and Kynard 1986). All territories were considered stable if positions were held static for three consecutive observation periods. We replicated this with a new group of fish five times. Final densities ranged from 6 to 10. The modal density of eight fish per channel was chosen as the high density. We halved this to four individuals in the low-density channels.

Observation protocol

Fish in all 12 channels were observed daily, with observation periods covering 24 h. Channels and focal fish were chosen at random. Visual night observations were conducted under deep-red illumination (wavelengths greater than 640 nm). Three Sylvania S14 lamps (11 W, 130 V, deep red; Albright Lighting Ltd., Victoria, B.C.) illuminated each channel from a height of 1 m. The spectral output of the lamp was chosen to minimize the stimulation of the red-sensitive cone photoreceptors found in salmonids, thus mimicking night conditions (peak absorbance 576 nm; Hawryshyn and Harosi 1994). Because the spectrum of these lights capitalized on the absorbance differences between salmonid and human eyes, we were able to visually observe fish in what they perceived as relative darkness.

Over each 10-day experimental period, observation sessions of focal fish lasted 5 min (total times given in Table 2). During this period, all activities undertaken by the focal fish were recorded in one of three categories: forage, agonism, and cruise. These were defined, respectively, as the number of prey consumed; counts of attacks, charges, or chases performed or received by focal fish; and counts of nondirectional movement of focal fish. All interspecific-agonism values were corrected, to account for species asymmetry in mixed channels. A focal fish had three potential intraspecific and four interspecific targets.

Data analysis

All fish were weighed and measured at the end of each experiment, to calculate the competition coefficients. Our behavioural data are non-independent (only one behaviour could be executed at a time to the exclusion of all others), so we used principal-component analysis (PCA) on the correlation matrix, to reduce the number of variables (McPeek 1990). The principal component (PC) scores were used as dependent variables in a stepwise generalized linear model (GLM). The stepwise GLM adds and subtracts main and interaction effects (experiment, density, forage level, species), to determine which subset of variables combine to give the simplest adequate model of the PC based on Akaike's (1974) information-criterion value. The best-fit models were further simplified by eliminating any terms with a Mallow's (1973) C_p value of less than one. The terms of each GLM were then subjected to a fixed-effect analysis of variance (ANOVA) and tested for significance. A multivariate analysis of variance (MANOVA) was not necessary, as the PCs are, by definition, uncorrelated. All analyses were performed in S-PLUS version 4.5 (Mathsoft International, Inc., Seattle, Wash.).

Results

Overall we found that steelhead cruised 4.5 times more than Atlantic salmon and committed five acts of agonism for each similar act executed by Atlantic salmon (Table 2). Over the course of each of the three experiments, both species lost weight and grew only modestly in length (Table 2).

Steelhead were 2.1 times more likely to be agonistic towards a conspecific than towards an Atlantic salmon. Atlantic salmon were 2.2 times more likely to attack a steelhead

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Table 3. Per capita weight change of Atlantic salmon and steelhead at low- and high-ration levels and different densities, and mean agonism, forage, and cruise counts per 5-min observation period at different densities.

	Steelhead			Atlantic salmon			
	Low density	High density	Mixed	Low density	High density	Mixed	p
Δweight (g)							
Low ration	–0.093	–0.064	–0.026	–0.052	–0.075	–0.062	—
High ration	–0.047	–0.057	–0.004	0.003	–0.097	–0.069	—
Agonism							
Intraspecific	1.230	2.430	1.003	0.250	0.310	0.082	<0.001*
Interspecific	—	—	0.470	—	—	0.180	0.18
Forage	3.34	3.26	3.21	2.63	3.57	2.75	0.67
Cruise	8.40	6.54	7.50	2.51	1.68	1.01	<0.001*

* p value significant at <0.05.

than a conspecific ("mixed" columns, Table 3). Interspecific agonism in Atlantic salmon increased markedly with age, while in steelhead, it peaked during experiment 2 and declined sharply in experiment 3, when Atlantic salmon were larger than steelhead (Table 1). Number and types of clips used for individual identification were evenly distributed among species and treatments. No relationship between clips and performance (weight change) was observed in a multiple regression analysis ($p > 0.08$).

Nine fish (3.8%) were lost owing to mortality (four Atlantic salmon and five steelhead). All but one individual of each species were accounted for—they had jumped out of the channel over or through a retaining screen. Calculations were adjusted to account for asymmetric densities due to mortality.

Behaviour at different densities

High-density treatments increased the level of agonism in steelhead ($p < 0.001$) (Table 3) but made little difference to foraging and cruising rates (Table 3). A similar but less pronounced pattern was seen with Atlantic salmon: agonism increased at high density ($p = 0.033$) (Table 3), foraging showed only moderate change, and cruising dropped markedly (Table 3).

In mixed channels, steelhead targeted conspecifics more than twice as often as Atlantic salmon, while showing little change in other behaviours (Table 3). Atlantic salmon sympatric with steelhead showed a 67% reduction in intraspecific agonism (Atlantic salmon in low-density channels vs. Atlantic salmon in mixed channels; Table 3) and a 2.2:1 bias towards interspecific agonism. Little change was noted in Atlantic salmon foraging rate and, as in the intraspecific high density treatment, cruise rate dropped markedly.

Principal-component analyses

Intraspecific and interspecific channels were examined separately, owing to the differences in competitive relationships in each.

Intraspecific

The first three PCs accounted for 80% of the total variation (Table 4). The first PC (PC1) is related to agonism. Fish in channels with a high frequency of agonism were likely to display low growth and reduced foraging rates. The second PC (PC2) is correlated with activity levels. More sedentary fish were less agonistic and more likely to show reduced growth. The third PCS (PC3) shows a residual positive correlation between foraging and agonism.

Interspecific

The first three PCs accounted for 91% of the total variation (Table 4). PC1 is activity with a positive correlation among intra- and inter-specific agonism and cruising. PC2 reveals a negative relationship among growth and cruising—fish with reduced growth rates are more sedentary. PC3, as with the intraspecific PC scores, shows a residual positive relationship between foraging and intraspecific agonism. Increased foraging comes at a cost of increased intraspecific agonism, regardless of whether the individual is in a single-species or mixed channel.

Treatment effects on behaviour

Intraspecific

Agonism (PC1) increased later in the season as the fish grew. Steelhead were more aggressive than Atlantic salmon (Table 5), but the difference decreased with time (block). Steelhead were more active than Atlantic salmon (PC2) under all conditions.

Interspecific

In sympatry as in allopatry, steelhead were more active and aggressive than Atlantic salmon (Table 6) under all conditions.

Diurnal versus nocturnal activity

At night, steelhead increased their rates of both intra- and inter-specific agonism and markedly reduced their foraging and, to a lesser extent, cruising (Table 7). Atlantic salmon increased intraspecific agonism at night by 122% and interspecific agonism by 32%. Foraging also increased slightly, but cruising activity dropped dramatically (Table 7).

Resident versus challenger effects

Resident–challenger status had a pre-eminent effect on predicting performance. Resident fish outperformed challengers in all instances, regardless of other treatment effects (Table 8). In the simplest terms, on average across all fish, residents gained weight and challengers lost weight (Fig. 3).

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Table 4. Loadings for intra- and inter-specific principal-component analysis.

	Principal component					
	1	2	3	4	5	6
Intraspecific loadings						
Cruise	0.191	–0.838	–0.046	0.411	0.304	
Forage	–0.450	0.046	0.835	0.269	0.147	
Δlength	–0.498	–0.313	–0.136	–0.700	0.396	
Δweight	–0.532	–0.333	–0.163	0.122	–0.751	
Intraspecific agonism	0.479	–0.289	0.519	–0.503	–0.405	
% cumulative variation	37.6	62.7	80.0	92.0	100.0	
Interspecific loadings						
Cruise	0.477	–0.437	–0.137	–0.280	–0.001	0.696
Forage	–0.116	–0.144	0.932	–0.100	–0.264	0.130
Δlength	–0.394	–0.471	–0.121	0.725	–0.154	0.241
Δweight	–0.026	–0.707	–0.117	–0.336	–0.175	–0.585
Intraspecific agonism	0.530	–0.199	0.285	0.420	0.596	–0.259
Interspecific agonism	0.567	0.164	–0.051	0.311	–0.722	–0.176
% cumulative variation	42.8	73.9	91.2	96.6	99.5	100

Note: The percent cumulative variation accounted for by the addition of each principle component is given below each set of loading values.

Table 5. ANOVA of terms associated with the minimum adequate model of intraspecific principal component (PC) scores.

	df	SS	*F*	*p*
Agonism (PC1)				
Block	2	27.18	14.34	0.000
Density	2	1.29	0.68	0.510
Species	1	10.82	11.43	0.002
Block:density	4	1.00	1.05	0.310
Residuals	26	27.46		
Activity (PC2)				
Species	1	26.51	48.35	0.000
Residuals	34	18.64		
Foraging and agonism (PC3)				
Block	2	21.80	46.52	0.000
Density	2	1.19	2.54	0.096
Species	1	1.15	4.89	0.035
Residuals	30	7.03		

Table 6. ANOVA of terms associated with the minimum adequate model of interspecific principle component (PC) scores.

	df	SS	*F*	*p*
Agonism (PC1)				
Species	1	13.72	8.01	0.018
Residuals	10	17.13		
Growth (PC2)				
Species	1	11.22	10.06	0.001
Residuals	10	11.15		
Foraging and agonism (PC3)				
Block	2	10.33	17.49	0.002
Species	1	0.17	0.59	0.468
Food level	1	0.01	0.02	0.886
Residuals	7	1.44		

This pattern was equally prominent in conspecific channels and mixed channels. Even when both residents and challengers lost weight, challengers lost at least twice as much weight as residents (Table 8). Forage level did not have a consistent effect, as low-ration fish did not always lose more weight than their high-ration counterparts (Table 8).

Resident steelhead showed better overall performance at high density, which was opposite to our a priori prediction (Table 8). Steelhead at high density lost only 0.007 and 0.004 g per capita in high- and low-forage channels, respectively, compared with 0.093 and 0.047 g per capita in high- and low-forage channels, respectively, at low density. We suspect that dominant individuals can be more effective at restricting access to profitable feeding areas when at low-density than when at high density. At high density, a dominant individual must defend a profitable position against seven other fish, while a dominant individual at low density has only three other fish to exclude. Therefore, owing to the diluted attention of the dominant fish, subordinates in the high-density channels had a greater number of foraging opportunities and, on average, gained more or lost less weight than their low-density counterparts.

The pattern of resident fish out-competing challengers was most obvious among those individuals that showed the greatest weight change—either positive or negative. The 20 fish (10% of the study population) that recorded the greatest gain or loss of weight were examined for a pattern that might predict the observed dramatic change in weight. Of the five potential predictive factors, resident–challenger status was highly significant ($F_{[1,14]} = 9.8$, $p = 0.011$), whereas all other factors shared no predictive power (all $F < 1.0$).

Coefficients of competition

Steelhead showed better per capita mass change at low forage, whereas Atlantic salmon performed better in high-forage situations (Table 9). The high degree of steelhead intraspecific agonism is reflected in the competition coefficients. At the low forage rate, the per capita effect of steelhead on steelhead (a_{ss}) is roughly double that exerted by Atlantic salmon on steelhead (a_{as}) and increases to four times at high forage levels. The effect of Atlantic salmon on

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Table 7. Behaviour counts observed during day (06:30–19:59) and night (20:00–06:29) and percent change in activities from day to night.

	Steelhead			Atlantic salmon		
	Day	Night	% change	Day	Night	% change
Intraspecific agonism	1.02	1.49	+46	0.09	0.20	+122
Interspecific agonism	0.60	0.74	+23	0.23	0.14	+39
Forage	4.53	1.91	–58	1.91	2.46	+29
Cruise	6.53	5.41	–17	2.92	1.14	–61
No. of observation sessions	243	116	—	211	111	—

Note: Data are from all three experiments and counts are standardized per 5-min observation session.

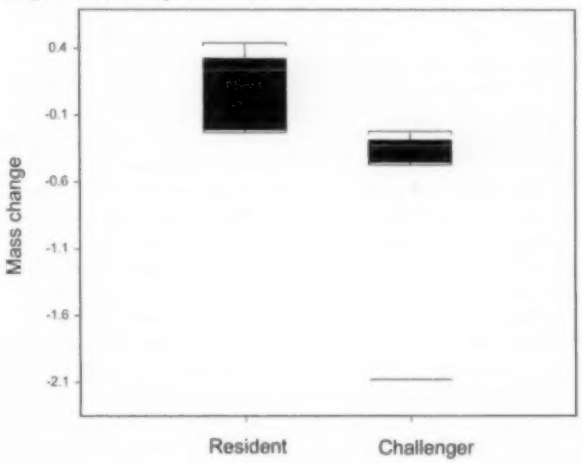
Table 8. Per capita change in mass (g) of resident versus challenger fish; data are arranged to contrast the effects of density and ration.

	Steelhead			Atlantic salmon		
	Resident	Challenger	% change	Resident	Challenger	% change
Low ration						
Intraspecific low density	–0.093	—	—	–0.052	—	—
Intraspecific high density	–0.007	–0.122	–1643	–0.061	–0.090	–48
Interspecific (high) density	–0.016	–0.036	–125	0.110	–0.235	–314
High ration						
Intraspecific low density	–0.047	—	—	0.003	—	—
Intraspecific high density	–0.004	–0.110	–2650	–0.058	–0.137	–136
Interspecific (high) density	0.029	–0.021	–172	0.071	–0.209	–394

itself is double that of steelhead on Atlantic salmon at the low forage level, but this difference diminishes at the high forage rate.

The coefficients of competition are more informative when analyzed separately for resident and challenger effects (Table 10). For steelhead, the direction of effect between resident and challenger fish is greatest in intraspecific channels, reflecting the dominant role of intraspecific agonism in steelhead performance. For Atlantic salmon, the distinction is not nearly so great. However, in mixed channels, Atlantic salmon do well as residents when challenged by steelhead, but relatively poorly as challengers (Table 10).

Fig. 3. Box plot of relative weight change of resident and challenger fish (both species combined).



Discussion

Atlantic salmon and steelhead have only rarely come into contact in the wild and so there are few studies contrasting their competitive ability in sympatry. The few studies that have explicitly addressed this issue concluded that steelhead and Atlantic salmon are likely to compete for resources with relative success that is likely to vary with environmental parameters (Gibson 1981; Hearn and Kynard 1986; Jones and Stanfield 1993). Here, steelhead performance was superior relative to Atlantic salmon, but intraspecific (a_{ss}), not interspecific (a_{as}) agonism is the greater influence on performance. The average per capita competitive influence from an Atlantic salmon across all treatments is less than half that from another steelhead. However, the resident–challenger status of the individual greatly affects this generalization.

Greater aggression does not automatically translate to superior competitive ability. Interspecific competition can only be evaluated relative to intraspecific competition (Underwood 1986; Fausch 1997). Steelhead were greater than five times more aggressive than Atlantic salmon, but targeted other steelhead 2.1:1 over Atlantic salmon in mixed channels. In the same channels, Atlantic salmon showed an agonistic bias of 2.2:1 towards steelhead. As a result, replacement of steelhead with Atlantic salmon had little net effect on the number of agonistic interactions in which an individual steelhead was likely to be involved. Overall, Atlantic salmon did not perform as well as steelhead, but did show superior performance as residents.

Many fish lost mass over the course of the experiments. The sparse experimental environment, minimal depth, and limiting forage supply are likely the causes of this observation. A similar study of brown trout (*Salmo trutta*) found

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Table 9. Coefficients of competition (a) of steelhead and Atlantic salmon at high and low forage levels.

	a_{ss}	a_{as}	a_{aa}	a_{sa}
Low ration	+0.029	+0.067	–0.023	–0.010
High ration	–0.010	+0.043	–0.100	–0.072

Note: a_{ss}, steelhead intraspecific; a_{as}, Atlantic salmon – steelhead interspecific; a_{aa}, Atlantic salmon intraspecific; a_{sa}, steelhead – Atlantic salmon interspecific.

Table 10. Coefficients of competition (a) of resident versus challenger steelhead and Atlantic salmon at high and low forage levels.

	Steelhead		Atlantic salmon	
	Resident	Challenger	Resident	Challenger
Low ration				
a_{ss}	+0.086	–0.029	—	—
a_{as}	+0.077	+0.057	—	—
a_{aa}	—	—	–0.009	–0.038
a_{sa}	—	—	+0.162	–0.183
High ration				
a_{ss}	+0.043	–0.063	—	—
a_{as}	+0.076	+0.026	—	—
a_{aa}	—	—	–0.061	–0.140
a_{sa}	—	—	+0.068	–0.212

Note: a_{ss}, steelhead intraspecific; a_{as}, Atlantic salmon – steelhead interspecific; a_{aa}, Atlantic salmon intraspecific; a_{sa}, steelhead – Atlantic salmon interspecific.

that only fish in channels augmented with woody debris with high forage rates gained mass. Those in control channels (not augmented, high and low forage) and in augmented channels at low forage rates all lost mass (Sundbaum and Näslund 1998). The lack of sufficient structure to provide visual isolation resulted in increased activity levels and corresponding energy expenditure. Greater augmentation of our channels may have served to reduce overall energy expenditure. Also, our channels were shallow (8 cm) and may have artificially amplified interspecific agonism by not allowing effective partitioning of the water column. Atlantic salmon were usually found in contact with the substrate, while steelhead remained in the water column. If the channels were deeper, it is possible that microhabitat partitioning might reduce interactions and result in lower energy expenditure. Finally, we observed that fish of both species did not pursue forage after it was in contact with the substrate. Since forage items were slightly negatively buoyant, they did occasionally drop from the column before being consumed, resulting in a net shortfall of forage (food was allotted to channels based on the assumption of a near 100% foraging efficiency and on energy budgets of relatively inactive aquaculture fish). Also, unlike the situation in the wild, the option of emigrating from vigorously contested areas was not an option here. These factors do detract from the "naturalness" of our simulations, but modifications to ameliorate them would reduce interspecific interactions and thus biotic resistance to Atlantic salmon. Our experimental conditions are likely harsher, in terms of intra- and inter-specific competition, than may be expected in the wild and, therefore, estimates of Atlantic salmon performance are, if anything, conservative.

Atlantic salmon showed a marked increase in aggression and foraging at night. Wild Atlantic salmon have demonstrated increased nocturnal activity (Gries et al. 1997). Our experimental design did not allow us to partition Atlantic salmon nocturnal performance by residents and challengers but it is possible that overall poor diurnal performance could be ameliorated by a combination of increased nocturnal Atlantic salmon agonism and foraging activity and reduced nocturnal foraging and cruising by steelhead.

Competitive exclusion has been suggested as a potential factor affecting some Atlantic salmon augmentation–re-establishment programs (Kennedy and Strange 1986). In British Columbia, adult Atlantic salmon are, at times, numerous in many coastal rivers, particularly in northern Vancouver Island (Thomson and Candy 1998). Competitive exclusion by natives during the juvenile stage and a suggested but unidentified deficiency in Atlantic salmon colonization ability have been argued as reasons escapees are not likely to colonize (Needham 1995). In our experiments, Atlantic salmon did not perform well when "released" (i.e., challengers) into habitat already occupied by steelhead. However, when juvenile Atlantic salmon are allowed a residency period of 3 days, the ability to resist competitive intrusion of both steelhead and other Atlantic salmon competitors increases. This phenomenon was not limited to Atlantic salmon; resident steelhead likewise outperformed both intra- and inter-specific challengers. In some cases, the difference in performance was dramatic—up to 2650% improvement was observed between resident and challenger steelhead at high ration. In all cases, the differences were so large that prior residency became the only meaningful predictor of performance. Re-analysis of the data taking this into consideration shows that the top-performing group overall are resident Atlantic salmon in mixed channels at low food ration. If Atlantic salmon are resistant to interspecific competition after a short settlement period in isolation, habitats in the wild underutilized by niche equivalent competitors are more likely to be colonized.

The asymmetry of performance observed between residents and challengers is intriguing but the phenomenon is not new. Braddock (1949) described the "prior residence" effect in work with the platyfish (*Platypoecilus maculatus*). Significant prior residency advantage has been documented in juvenile Atlantic salmon with a separation of as little as 1 day between the introduction of challengers to conspecific residents (Huntingford and Garcia de Leaniz 1997), significantly less separation time than the 3 days used here. Prior residency has also been found to be a significant predictor of success for juvenile Atlantic salmon (Cutts et al. 1999*a*, 1999*b*; O'Connor et al. 2000). The prior residency effect may be widespread in salmonids, as both underyearling brown trout (*S. trutta*) and chinook salmon (*O. tshawytscha*) also show a significant prior residency advantage in interspecific competition (Glova and Field-Dodgson 1995).

In addition to other teleosts (Rauch 1996; Itzkowitz et al. 1998), prior-residency effects have been described in a wide array of taxa (Sandell and Smith 1991; Baugh and Forester 1994; Figler et al. 1999). The phenomenon is hypothesized to be the result of a resident's knowledge of the territory and, thus, its potential value. Armed with this information, a

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resident's defence of the territory is likely to be more vigorous than a naive challenger's attempts to usurp it (Krebs 1982). Further, residents may be habituated to the test environment, while challengers may be more fearful and therefore less likely to engage in aggressive acts (Figler and Einhorn 1983). By augmenting the physical environment in the steelhead holding tank, we tried to minimize the physical differences between it and the experimental channels. Atlantic salmon did not receive such treatment (the holding tank was intentionally left bare, to simulate culture conditions); therefore, if there were negative effects in transferring fish between holding and experimental environments, we expect it affected Atlantic salmon to a greater degree than steelhead.

Residence effects are usually detected when competitors are of similar size. Therefore, residence effects may be more prominent in intraspecific competitions, as contestants are more likely to be similarly sized. Interspecific life-history differences are more likely to result in one species dominating, owing to a size advantage that may or may not be temporally stable. For instance Glova and Field-Dodgson (1995) observed that species dominance changed with time as the size advantage of earlier-emerging chinook dissipated. The threshold intraspecific size difference at which prior-residence advantage can be overcome is variable and has been estimated to be 10% total length for blennies (*Parablennius marmoreus*; Rauch 1996) and 6% for coho salmon (*O. kisutch*; Rhodes and Quinn 1998). Although the fish used in the majority of our experiments were standardized for size, Atlantic salmon were, on average, larger than steelhead; however, because each was maintained on different forage, direct comparisons are not possible. Field observations suggest that Atlantic salmon may have a size-at-age advantage over steelhead. A comparison of wild-reared Atlantic salmon and steelhead of similar ages from the Tsitika River, British Columbia, showed that Atlantic salmon were more than 50 and 100% larger than steelhead at 0+ and 1+ stages, respectively (Volpe et al. 2000). Atlantic salmon eggs require longer incubation than steelhead eggs—500 and 375 degree-days, respectively (Jobling 1995)—which translates into an approximately 25 day shorter incubation for steelhead eggs at 5°C. However, Atlantic salmon generally spawn in the fall or early winter (Scott and Scott 1988), whereas steelhead generally spawn in the spring (Scott and Crossman 1973). There is a high probability that, by spawning months ahead of steelhead, juvenile Atlantic salmon could exhibit a size–development advantage sufficient to overcome any advantage to steelhead through faster embryonic development. To date, only a single feral population has been studied, but the significantly larger size-at-age of the juvenile Atlantic salmon relative to sympatric steelhead (Volpe et al. 2000) supports this prediction.

Attempts to introduce Atlantic salmon to southern British Columbian rivers in the early half of this century failed. During this period (1905–1933; Carl and Guiguet 1958), coastal river systems would have been at or near saturation and vacant niche space would have been sparse, with suitable habitat saturated with native residents. We have demonstrated that Atlantic salmon do not perform well when introduced under such conditions. However, these conditions no longer exist. Steelhead populations in 12 of the 19 major river systems on Vancouver Island's east coast have been classified as "high risk"—population estimates over the past decade have been less than 20% of their long-term means (Bruce Ward, B.C. Ministry of Fisheries, University of British Columbia, 2204 Main Mall, Vancouver, BC V6T 1Z4, Canada, personal communication). The situation is much the same across the entire coast of British Columbia, as niches broaden in response to severely depressed and, in some cases, locally extirpated native populations (Slaney et al. 1996). Unlike the situation earlier this century, suitable rearing habitat is no longer likely to be limiting, and the potential for successful Atlantic salmon colonization has increased as a result. Juvenile Atlantic salmon may come to occupy such habitat directly, via escape from stream-side hatcheries or lake rearing pens (McKinnell et al. 1997), or through natural reproduction of free-ranging adults (Volpe et al. 2000).

Temporal segregation benefiting Atlantic salmon may result from life-history differences between Atlantic salmon and native salmonids in British Columbia. Atlantic salmon show considerable life-history variability across the native range. Spawning time usually ranges from September to December (Scott and Scott 1988) but may extend into March (Garcia de Leániz et al.1987). Free-ranging Atlantic salmon observed in British Columbian rivers do not begin to show spawning colouration until late fall, suggesting a spawning time near the end of this distribution (Volpe 1998, 1999, 2000). In a pilot experiment to assess the spawning capability of aquaculture-production fish, none of the 50 Atlantic salmon used displayed spawning characters (physical or behavioural) until mid-January (Volpe et al. 2001). Based on these data, we suggest that much of Atlantic salmon spawning activity may occur after most of the spawning activity of the five fall-spawning native *Oncorhynchus* species but before that of spring-spawning steelhead. If so, native adult spawner densities would be low at this time, resulting in minimal competition for redd sites. Atlantic salmon may superimpose their redds on those of earlier-spawning Pacific salmon or have theirs superimposed by those of spring-spawning steelhead. Superimposition has been demonstrated to be a significant factor in determining spawning success in space-limited systems (Hayes 1987). Currently in coastal British Columbia, low numbers of both Atlantic salmon and steelhead suggest superimposition is not, for the time being, likely to be a significant issue.

Early deposition of eggs from a successful Atlantic salmon mating would see progeny emerging from the redd in advance of steelhead. The Atlantic salmon used in this study hatched more than 2 months before the steelhead. If successful establishment of Atlantic salmon depends, in part, on settlement in isolation, a 2-month head start on the competition would prove to be a significant factor.

These data also have implications for enhancement and other management initiatives using stocked fish. Hatchery-reared fish introduced as part of wild stock augmentation programs have been shown to be deficient in numerous characters important for survival and fitness (Olla et al. 1998; Utter 1998). However, we are not aware of any such studies that have explicitly tested the role of residency in calibrating the performance of wild and introduced cultured stocks. The observed reduction in performance of hatchery-reared fish may be partly explained by their simply being challengers. In our

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simple test environment, an acclimatization period of only 3 days was necessary to produce significant performance differences in both species during intra- as well as inter-specific trials. Hatchery-reared fish released during augmentation programs may face similar challenges in the wild.

Our data demonstrate that Atlantic salmon are capable of colonizing vacant or underutilized habitat and of successfully defending that habitat against subsequent challenges from steelhead. These data also suggest that predicting the fate of feral Atlantic salmon in coastal British Columbia can be accomplished only by considering the native salmonid demographics and physical parameters of each contaminated system.

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Testing mechanistic explanations of observed correlations between environmental factors and marine fisheries

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Abstract: Based on observed correlations, marine fisheries are often hypothesized to depend on environmental factors. Since correlations are unreliable as a predictive tool, it is desirable to seek mechanistic explanations for observed correlations. This paper considers methods available for testing such mechanistic explanations. As a specific example, we consider the optimal stability window, proposed as a mechanistic explanation of observed correlations between the survival of North Pacific salmon stocks and the state of the atmosphere over the North Pacific in winter, as applied to the coastal waters and fisheries of southern British Columbia, Canada.

Résumé : À cause des corrélations que l'on observe entre les facteurs de l'environnement et les pêches marines, on émet souvent l'hypothèse qu'il existe un lien de dépendance entre les deux. Cependant, comme les corrélations ne peuvent servir d'outil fiable pour établir des prédictions, il faut rechercher des explications mécanistes aux corrélations observées. Nous présentons ici un examen des méthodes disponibles pour tester de telles explications mécanistes. L'exemple précis que nous étudions est la « fenêtre de stabilité maximale » qui a été proposée comme explication mécaniste des corrélations qui existent entre la survie des stocks de saumons du Pacifique Nord et les conditions de l'atmosphère au-dessus du Pacifique Nord en hiver et nous l'appliquons aux eaux côtières et aux pêches du sud de la Colombie-Britannique, Canada.

[Traduit par la Rédaction]

Introduction

The study of the effects of climate variation on fisheries has depended heavily on correlations between fisheries data, generally catch, and some environmental variable(s). While correlations are suggestive, they are notoriously unreliable as predictive tools (Kinsman 1957). Without knowing the mechanistic connections between the variables being correlated, we cannot have confidence that the correlations will continue, and indeed they often fail abruptly. It is thus essential to move on to a process in which two things will happen. First, we will use correlations less as predictive measures and more as clues that signal and constrain possible mechanistic connections. Second, we will seek to test hypothesized connections.

An example of the first step in such a process is the optimal stability window proposed by Gargett (1997) as a mechanistic explanation of two correlational clues: first, positive correlation (Beamish and Bouillon 1993) on decadal time scales between North Pacific all-nation salmon catch and an index of the average strength of the wintertime Aleutian Low pressure system and, second, negative correlation (Francis and Sibley 1991) between survival of northern (Alaska) and southern (Washington, Oregon, and northern California) stocks. Gargett (1997) argued that variations in atmospheric circulation between strong and weak phases of the Aleutian Low produce in-phase changes in coastal water column stability through coupled changes in freshwater input to the subpolar coastal ocean and wind-driven boundary upwelling in the subtropical coastal ocean. Through stability-induced changes in nutrient and light supplies to primary production, reflected in secondary production, in-phase variation of coastal stability in the eastern North Pacific translates into conditions favoring survival of juveniles entering the coastal ocean in the northern (southern) part of the salmonid range during strong (weak) Aleutian Lows, thus accounting for both correlational clues (for further details, see Gargett 1997).

Using this mechanism as an example, the present paper investigates methods for the second step, testing. To focus discussion, we consider the coastal waters and salmon stocks of southern British Columbia, Canada (Fig. 1), both offshore waters along the western coast of Vancouver Island and protected waters inside the Strait of Georgia.

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Methods

Stability time series from in-water data

The possibility of obtaining adequate time series from CTD/bottle data inventories is explored using a test area just off the mouth of Juan de Fuca Strait (Fig. 1). This area is as well sampled as any region of the British Columbia coast because it includes the inner end of "Line P" (a line of stations sampled a minimum of three or four times per year since 1956) as well as part of a more recent grid of repeated coastal observations. Density

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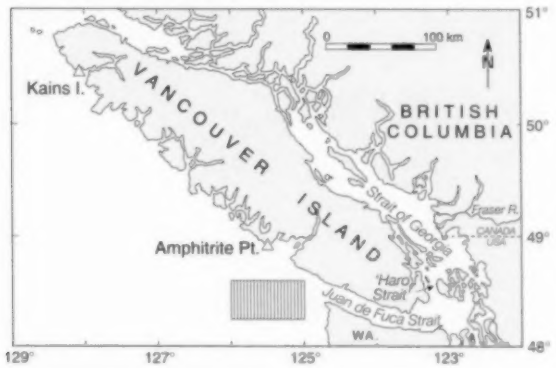
Fig. 1. Map of southern coastal British Columbia, Canada, showing the area (vertical shading) in which historical CTD/bottle data were composited, the locations (triangles) of two lighthouse shore stations, and the regions (Strait of Georgia, "Haro Strait," and Juan de Fuca Strait) incorporated in a biophysical box model.



profiles are abstracted from data in the archives of the Institute of Ocean Sciences for a spring season defined as April–May–June, when phytoplankton growth should set the table for juvenile salmon first entering the ocean. Figure 2*a* shows values of upper (U) and lower (L) layer average densities (in σ_t units) from individual profiles: lines connect averages over the highly variable number of stations available during the spring season of a particular year. Near-surface stability (Fig. 2*b*) is quantified by

$$\frac{\Delta\sigma_t}{\Delta z} = \frac{\overline{(\sigma_L - \sigma_U)}}{(d_L - d_U)}$$

where σ and d are, respectively, layer-averaged density and depth and the overbar denotes an average over all available stations within a year.

Stability time series from surrogate data

If deep density remains constant, a surrogate time series for coastal water column stability can be obtained from measurements of surface density at shore stations. To test this possibility, we use surface density values calculated from routine daily measurements of surface temperature and salinity at the two coastal lighthouse stations shown in Fig. 1 (data available through Institute of Ocean Sciences web site http://www.pac.dfo-mpo.gc.ca/sci/pages/lighthousedata.htm), again averaging over the spring season.

Salmonid catch and survival data

Records of catch and escapement of chum salmon (*Oncorhynchus keta*) entering the ocean off the west coast of Vancouver Island from 1951 to 1981 are reported in Beacham (1984). As well, we use estimates of survival of Chilko Lake sockeye salmon (*Oncorhynchus nerka*) made by direct counts of the number of smolts leaving the lake each year and the number of adults returning (predominantly) 2 years later (M.F. Lapointe, Pacific Salmon Commission, Vancouver, B.C., personal communication).

Results

Hypothesis testing through retrospective time series of stability

For mechanisms operating over decadal time scales, retrospective testing requires data over similar time scales. For a water column property like stability, many coastal ocean time series are well sampled only for the past 20–30 years, a period that is only about a half "cycle" of the variations in salmon catch (Beamish and Bouillon 1993). Over longer periods, the historical time series of water column density from southern British Columbia coastal waters (Fig. 2*a*) illustrates lack of continuity as well as undersampling, i.e., the frequent sparseness of data points in earlier years that do have data, both features typical of other coastal locations where decadal time series exist.

The time series of stability derived from this in-water data is predictably noisy, especially before sampling density increased in the early 1980s. However (disregarding for the moment the large peak in 1959–1960), there is a suggestion that stratification was generally higher during the 1980s, when northern stocks produced very large catches, and lower in the 1960s, when northern yields were poor (fig. 7 in Beamish and Bouillon 1993). Curiously, there are three relatively well-sampled years in the late 1930s: water column stability at this time, another period of high northern catches, lies at levels similar to those of the 1980s. Using these correlations as a rough calibration, Fig. 2*b* suggests that optimal stability in this region is ~0.03 $kg \cdot m^{-3} \cdot m^{-1}$) and that a value of ~0.02 $kg \cdot m^{-3} \cdot m^{-1}$ is suboptimal at the low-stability end of a "window." At the beginning of the 1990s, stratification levels appear to have begun declining towards levels last seen in the 1960s (although this trend is somewhat obscured by temporary rises associated the various El Niño events of the 1990s), suggesting that during this period, coastal ocean conditions moved towards suboptimal for northern stocks.

We return now to the most obvious signal in this record, the major 1959–1960 event associated with a large decrease of surface layer density (due primarily to a decrease in salinity, augmented by a minor (20–30%) contribution from increased temperature). While impressive in magnitude, neither the spatial distribution nor the number of data points defining this feature is particularly satisfactory. The 1959 and 1960 averages include only six and three stations, respectively: of six in 1959, two were taken within 1 h of another in the same location and hence are effectively duplicates. Of the remaining independent data points, two of five and two of three, respectively, are located within the 100-m depth contour, so averages will be more heavily weighted to near-coast conditions than averages from years with more and (or) more homogeneously distributed samples. Compared with a year with a spatially even distribution of sampling sites, nearshore weighting of stations will tend to produce "unusually" low surface layer density because of the presence of a buoyant coastally trapped current driven by freshwater runoff (Thomson et al. 1989).

While the above discussion highlights problems associated with data that are sparsely and nonhomogeneously distributed in both time and space, it does not necessarily negate the occurrence of a high-stability event in near-coastal waters in 1959–1960: before rejecting this event as a sampling artifact, we have sought corroborating data. If surface layer density decreased significantly over a spatially extensive area, the change should be evident in the time series of surface density at the two lighthouse stations along the west coast of Vancouver Island, shown in Fig. 2*c*. Superimposed (heavy line) is surface layer density from the CTD/bottle

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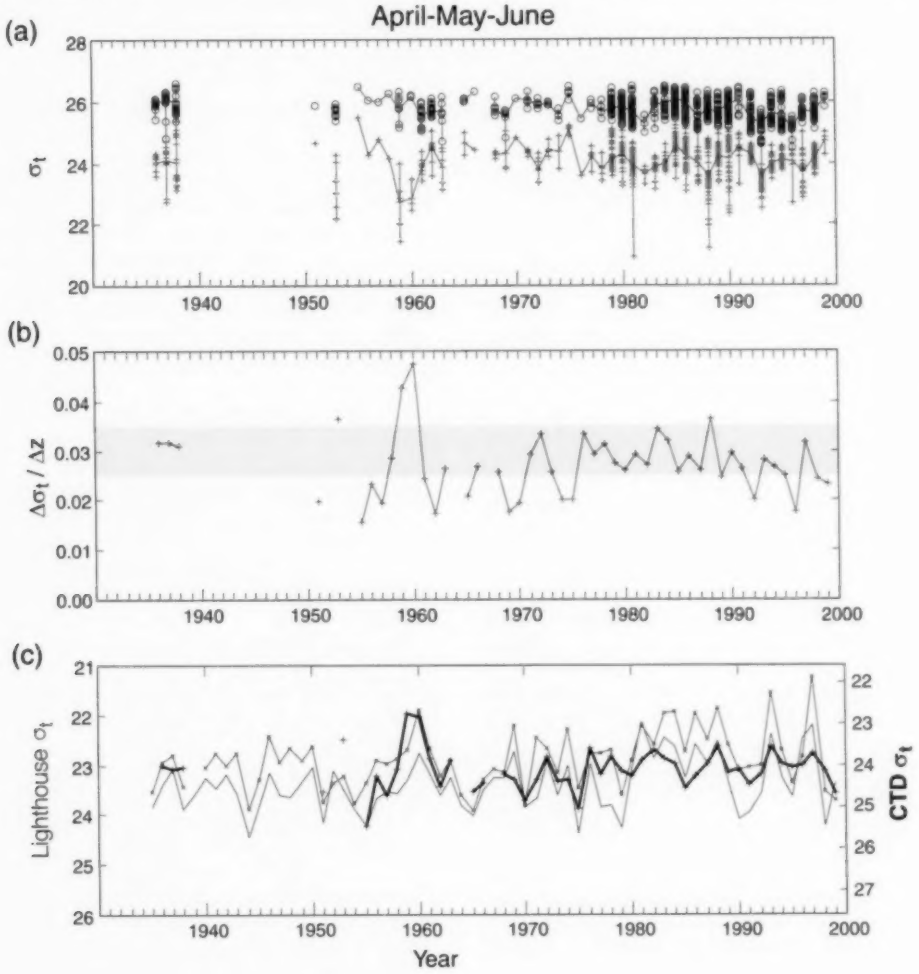
Fig. 2. (*a*) Density (σ_t) averaged over the upper (+, 0–20 m) and lower (○, 60–80 m) layers of CTD/bottle casts taken within the shaded region of Fig. 1 during the months of April, May, and June. Lines are averages over all available data in a given year. (*b*) Water column stratification parameter $\Delta\sigma_t/\Delta z$. Shading indicates a possible range of optimal stability for this region. (*c*) Comparison of time series of upper layer density from the historical CTD/bottle data (heavy line, +), offset to overlap April, May, and June averages of densities determined daily at lighthouse shore stations shown in Fig. 1 (light lines: upper, Amphitrite Point; lower, Kains Island).



data set (an offset of 1.6 σ_t units, chosen by eye, is necessary to produce this superposition because of the bias of the offshore CTD/bottle values to densities higher than those at the shore: all three series are plotted inversely, mimicking stability if lower layer densities remained constant). In 1960, both lighthouse stations, and particularly the southernmost station closest to the area of CTD/bottle data, show sharp maxima in inverse surface density, suggesting that the strong stability maximum seen in the offshore data during 1959 and 1960 may have extended over this larger spatial area. The additional measurements at the shore stations provide independent evidence that the 1959–1960 high-stability event in Fig. 2*b* is not an artifact (although the magnitude must still be considered unreliable because of the small sample size) and likely involved coastal waters along the entire length of Vancouver Island. Finally, consulting the historical record, we realize that this stability event was likely associated with an El Niño extending from 1958 to 1960, which McGowan et al. (1998) called "...one of the largest in the past 80 years...."

Is there evidence for negative effects of this large coastal stability event on salmon stocks in southern British Columbia waters? There are few measurements of actual marine survival of salmonids; rather, most information is that of catch and escapement, the highly nonlinear results of a myriad of natural factors affecting the success of year-classes, as well as human interaction in their "management." Despite the uncertainties involved, catch is often used as a surrogate for marine survival; lacking other consistent records extending over decadal time scales, we continue this usage. Figure 3*a* is a time series of the catch of chum salmon stocks entering the coastal ocean off the west coast of Vancouver

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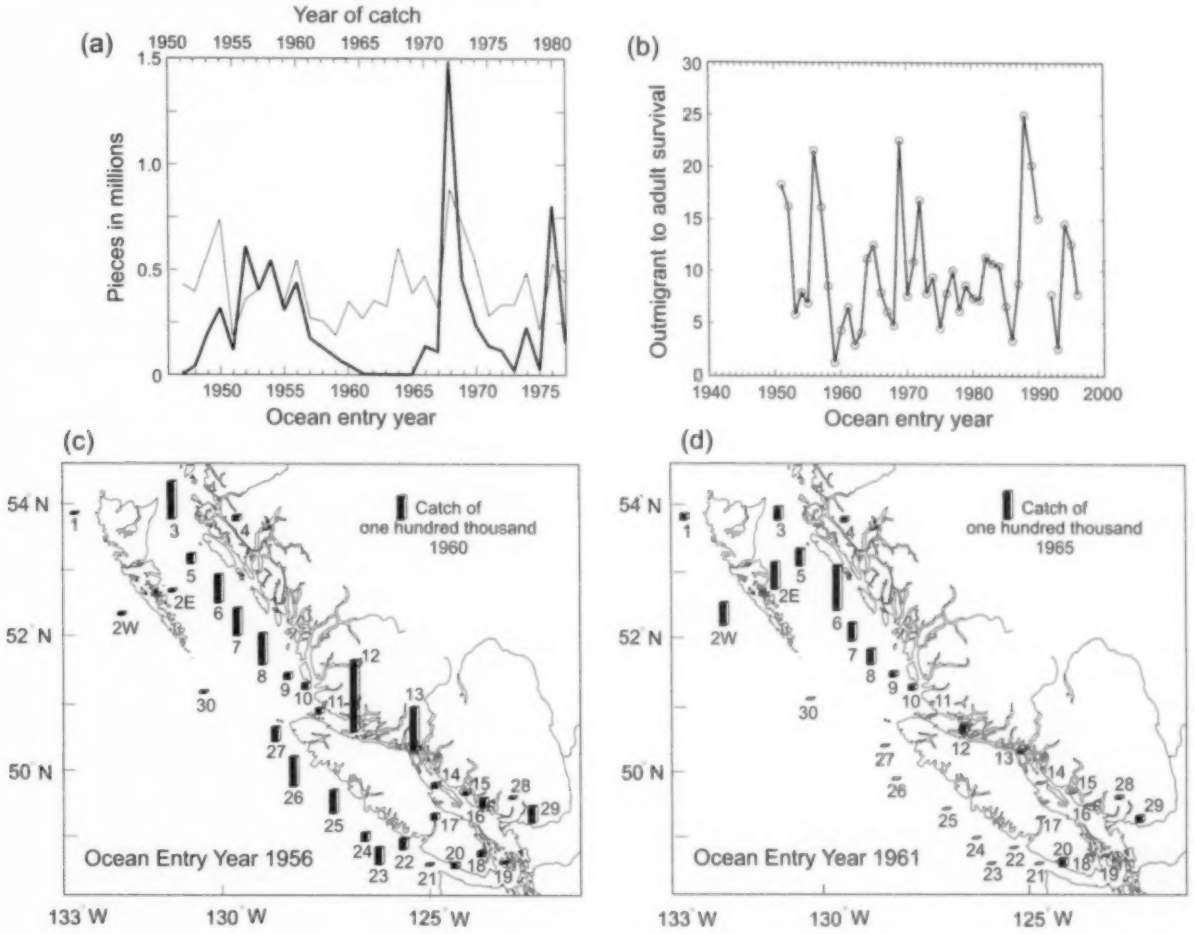
Fig. 3. (*a*) Historical record of catch (heavy line) and escapement (light line) of chum salmon on the west coast of Vancouver Island. Ocean entry year is year of catch minus 4 years, the average time at sea. (*b*) Survival of sockeye salmon rearing in Chilko Lake and entering the ocean in the Strait of Georgia. Geographical distribution, by statistical area (numbered), of catch of chum salmon that entered the ocean predominantly (*c*) during 1956 and (*d*) during 1961.



Island (Beacham 1984). Since chum salmon spend 3–5 years at sea (Hartt and Dell 1986), those entering the ocean during the El Niño years of 1958–1960 returned to the catch over the period from 1961 through 1965. An abrupt decrease in allowed catch began in 1961: the fishery was progressively reduced in subsequent years and finally shut down entirely for the five years from 1965 through 1969. In the light of Fig. 2*b*, a possible interpretation of this period is of an ecosystem highly overstressed by the unusual combination of at least two years (1959 and 1960) on the high-stability side of optimal, immediately followed by a prolonged period (the 1960s) on the low-stability side of optimal.

Other evidence indicates that this ecosystem stress affected other salmonid species and extended over a much larger area. Figure 3*b* shows the survival of Chilko Lake sockeye salmon, a different species entering the coastal ocean inside southern Vancouver Island. While there are many factors at play in determining interannual survival (including conditions during extensive river migrations of this stock to and from the ocean), note that the lowest survival in the entire record occurs for year-classes that went to sea during the 1958–1960 El Niño period, when coastal stability was high off Vancouver Island. (Since Fraser River sockeye salmon generally migrate out of the Strait of Georgia to the north, it would be preferable to relate their survival to a measurement of coastal stability further north, for example off the Queen Charlotte Islands: however, adequate data are not available in these more remote areas of the British Columbia coast.) Finally, Figs. 3*c* and 3*d* illustrate that the collapse of the chum salmon fishery documented in Fig. 3*a* was not confined to the west coast of Vancouver Island but extended throughout the coastal waters of southern British Columbia.

Hypothesis testing through surrogate time series of stability

Ocean temperature (and sometimes salinity) have been measured for several decades at various shore stations along

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the eastern boundary of the North Pacific. If these surface observations could be used as surrogate measures of stability, they would enormously enlarge the physical database available for testing the optimal window mechanism. Unfortunately, comparison of shore station surface density records with stability data from the offshore stations used in the previous section strongly suggests that shore density *cannot* be used to make reliable surrogate estimates of stability. For example, shore station inverse surface density (Fig. 2*c*) reached an all-time high during the El Niño of 1997: making the necessary assumption of fixed lower layer density, this would imply that coastal ocean stability was also at an historical high. However, layer densities calculated from the offshore stations (Fig. 2*a*) show that to a considerable extent, surface layer density changes are echoed at depth, so that changes in vertical density *difference*, i.e., in vertical stability, are more subtle than changes in surface layer density alone. In particular, although the "true" stability of Fig. 2*b* does have a local maximum in 1997, the value is of the same magnitude as that typical of the early 1980s rather than an historical extreme.

Hypothesis testing through biophysical models

Even if the sampling density achieved in the final 15 years of Fig. 2*a* were to be maintained over the decades that characterize major variation in the North Pacific ocean–atmosphere system, the British Columbia coast is not an ideal place in which to look for clear evidence of the optimal window effect. This is because British Columbia coastal waters are a complicated mixture of "pure" northern and southern regimes. Studies of anomalous precipitation associated with extreme states of the Aleutian Low (Cayan and Peterson 1989) indicate that precipitation in the Pacific Northwest, including southern British Columbia, is out of phase with precipitation in the pure northern regime (Alaska). In addition, the southern British Columbia outer coast is affected by seasonal (summer) upwelling rather than the year-round upwelling characteristic of a pure southern regime (southern Oregon). The results of the previous section are at least consistent with the hypothesis that the coastal ocean off the west coast of Vancouver Island functions as a northern regime (i.e., low survival rates associated with low stability). However, the transitional nature of this area means that the clearest signature of relationships between coastal stability and salmon survival would come from Alaskan and southern Oregon – northern Californian coastal waters. As in our study area, reliable water column data from these areas are not available over the required several decades: for example, the GAK1 Alaskan shelf CTD station has only been sampled intensively since 1990, while the long CALCOFI data set does not regularly sample northern Californian waters. Moreover, at least in our study region, we have demonstrated failure of the necessary assumption of constant deepwater density that underlies potential use of longer continuous time series of surface surrogates for stability. Thus, a conclusive observational test of the optimal window hypothesis awaits many years of well-sampled repeat CTD stations in appropriate areas.

In contrast, biophysical models enable immediate exploration of mechanistic explanations of observed correlations between environmental variables and marine fish stocks. As an example of such use of models, we focus a process modelling study on the Strait of Georgia (Fig. 1), the body of water between Vancouver Island and the mainland coasts of British Columbia and Washington State, and the region of first ocean contact for major Fraser River salmon stocks. We first determine what the window hypothesis predicts for this region. Cayan and Peterson (1989) demonstrated that when Alaska is wet (strong Aleutian Low), the Pacific Northwest is dry. Thus, assuming that the Strait of Georgia is a northern (light-limited) region, the optimal window predicts that Fraser stocks should vary out of phase with northern British Columbia and Alaska stocks. However, the Strait of Georgia actually functions as a *southern* regime because high stability associated with freshet of the Fraser River regularly leads to nutrient limitation of primary production in the late spring – early summer season when juvenile salmon first enter the coastal ocean. In a southern regime, low freshwater input associated with a strong Aleutian Low results in low stability and moves primary production towards more favorable conditions (see Gargett 1997). The window hypothesis thus predicts that Fraser River stocks entering the Strait of Georgia during favorable conditions associated with a strong Aleutian Low and migrating northwards where conditions continue favorable should be strong when northern stocks are strong. While this prediction agrees with observations for the dominant Fraser River sockeye stocks (Beamish et al. 1997), we will use a simple biophysical model to examine whether the Strait of Georgia system actually works this way.

Fig. 4. Schematic of a box model developed to test application of the optimal stability window to the Strait of Georgia region. Upper and lower boxes represent 0–50 and 50–200 m, respectively. The model includes estuarine circulation (unidirectional arrows) forced by freshwater input (FF) to the upper Strait of Georgia box and vertical mixing (bidirectional arrows). Salinity of the deep return flow in the lower Juan de Fuca Strait box is restored to Pacific salinity (SP).

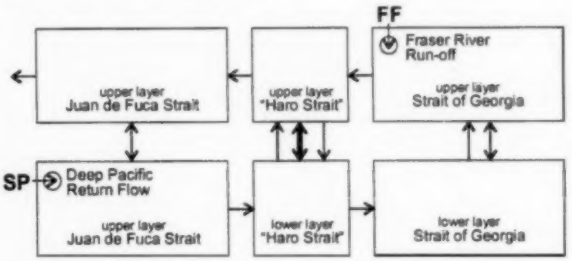

Figure 4 shows the physical configuration of a simple box model of the Strait of Georgia (G) and the relatively narrow passages that are its major connection to the offshore Pacific: first the many tidal mixing channels (H) labelled "Haro Strait" in Fig. 1 and then the broad Juan de Fuca Strait (F). We believe that such a minimalist model is (*i*) an appropriate first step in the study of decadal time scales (more complex models being too expensive to run for long periods of time), (*ii*) an essential tool for exploration of sensitivities to poorly known biological parameters, and (*iii*) the maximum degree of model complexity likely to be constrained by sparse available data.

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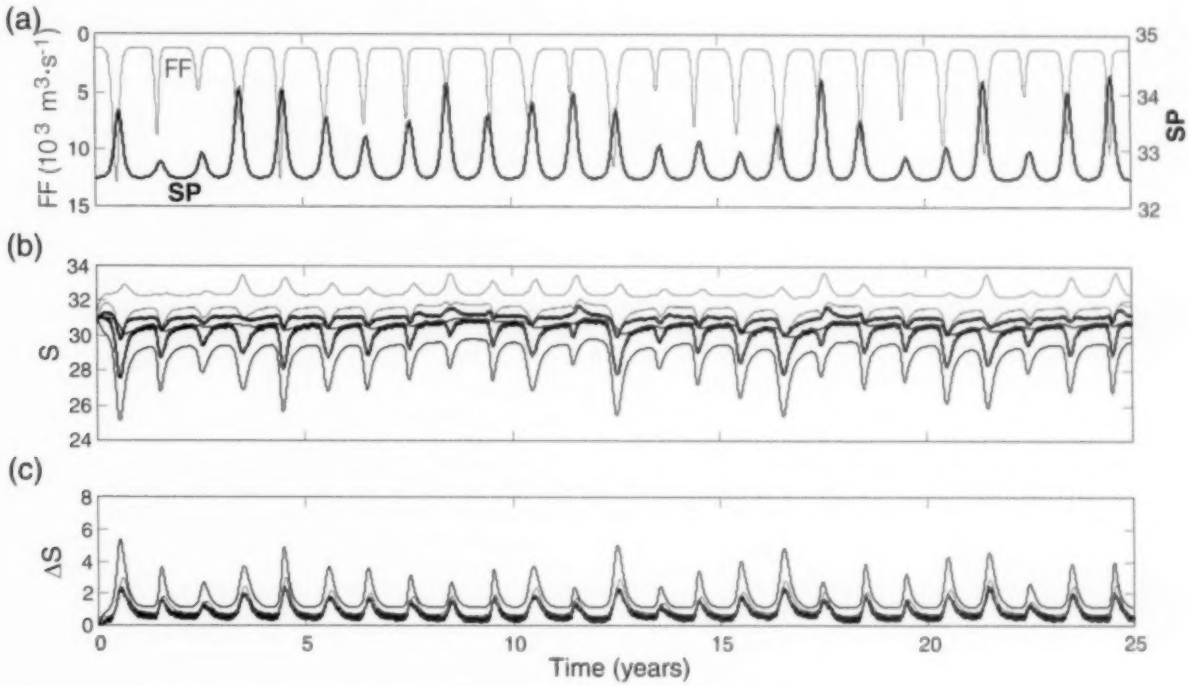
Fig. 5. Twenty-five-year simulation of salinity and stability fields produced by stochastic forcing of the physical model. (*a*) Stochastic physical forcing fields of Fraser River flow (FF, light line) and deep Pacific salinity (SP, heavy line). (*b*) Resulting time series of salinity S for the six model boxes. Line width identifies the basin (heavy lines, "Haro Strait"; medium lines, Strait of Georgia; light lines, Juan de Fuca Strait). In each basin pair, the upper layer has the lower S. (*c*) Stability, represented by the difference ΔS between upper and lower box salinities. Line width convention is the same as in Fig. 5*b*.



This estuarine box model, described in detail by Li et al. (1999) and subsequently referred to as the GHF model, is forced by strongly seasonal freshwater flow into the upper (0–50 m) G box, with salinity balance maintained by restoring salinity of the deep (50–200 m) F box to a "Pacific" salinity, which also varies seasonally as upwelling moves more saline water onto the British Columbia shelf in summer (Freeland and Denman 1982). Within the H boxes, strong tidal mixing with imposed variation due to the spring–neap tidal cycle (Griffin and LeBlond 1990) is modulated by model stability.

The single coefficient parameterizing the density-driven exchange flow is chosen to produce a response time to changes in freshwater flow of order 1 year (England et al. 1996). Forced with average annual cycles of freshwater flow and Pacific salinity based on observations, the model reproduces the observed seasonal cycle of average salinities in the six boxes. To investigate variability, the average solution is then perturbed by allowing significant parameters describing the physical forcing to vary within bounds, which are reasonably well determined from observations (Appendix A). As shown in Fig. 5, variability in physical forcing results in considerable interannual variability in the salinity fields, especially that of the upper Strait of Georgia, where stability varies by as much as a factor of 2.

When a simple nitrate–phytoplankton–zooplankton biological module (Li et al. 2000) is coupled to the steadily forced physical model, reasonable choices of biological parameters lead to an acceptable picture of the average annual biological cycles in the system (Fig. 6), as far as these are constrained by observations. In the Strait of Georgia, a spring bloom initiated by increasing light level is followed by a minimum in phytoplankton biomass caused partly by nutrient limitation and partly by zooplankton grazing; a secondary late summer peak of phytoplankton occurs as nitrate levels are renewed by input from offshore upwelling (see Appendix A for model implementation). Levels of phytoplankton are much lower (note the scale difference) in Haro Strait, where strong vertical mixing on spring tides causes regular losses to the unlit lower layer. With a very abbreviated spring bloom of much smaller magnitude than that in the Strait of Georgia, the ecosystem in Juan de Fuca Strait approaches high-nutrient, low-chlorophyll characteristics of the offshore Northeast Pacific (Miller 1993).

Figure 7 illustrates the response of this simple biological system to the interannual variation in physical properties shown in Fig. 5. Observationally reasonable interannual variability in the physical environment does not produce comparable variability in phytoplankton or zooplankton standing stocks in the Strait of Georgia, i.e., weaker (stronger) stratification does *not* produce significantly larger (smaller) zooplankton biomass as food for juvenile salmon. The model shows that the optimal window hypothesis is *not* valid for this system because local stratification-modulated mixing processes, on which the optimal window hypothesis is based, are not the dominant physical processes supplying nutrients to the

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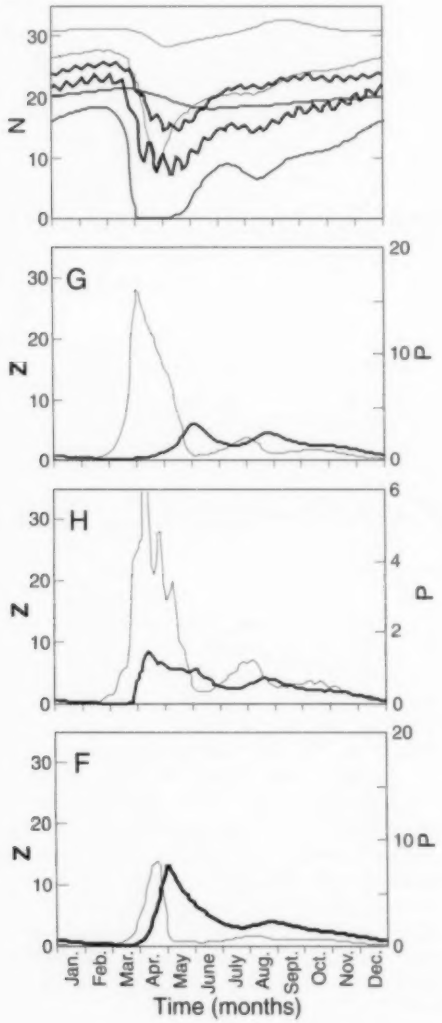
Fig. 6. Characteristic annual cycles of biological variables from a nitrate (N) – phytoplankton (P) – zooplankton (Z) model coupled to the physical box model of Fig. 4. Top panel: nitrate cycles in all six boxes. Line width convention is the same as in Fig. 5. All biological variables are in nitrate units of mmol $NO_3 \cdot m^{-3}$. Lower panels: upper layer values of modelled phytoplankton (light line) and zooplankton (heavy line) biomass in the Strait of Georgia (G), "Haro Strait" (H), and Juan de Fuca Strait (F).



euphotic zone in the Strait of Georgia. Instead, density-driven advection dominates vertical diffusion in supplying nutrients to this strongly estuarine system. Increased freshwater forcing of the upper Strait of Georgia produces an increased seaward pressure gradient, which drives stronger estuarine exchange flow. While the increased upwelling of nutrient-rich deep water within the Strait of Georgia thus supplies new nutrient to the surface layer in the Strait of Georgia at a rate that is higher than normal, the increased phytoplankton biomass suffers a higher than average advective loss in the outward-flowing surface layer. The opposite balancing of processes occurs when freshwater forcing is decreased. The net result is insensitivity of modelled phytoplankton and zooplankton biomass within the Strait of Georgia to variations in freshwater forcing of magnitudes comparable with those that might be expected due to decadal variability in the wintertime Aleutian Low pressure system.

Nevertheless, Fraser River salmon stocks *do* vary dramatically, and the variations *are* apparently correlated with atmosphere–ocean variability on decadal time scales, with the same phase as northern stocks. If the optimal window hypothesis is not the explanation, what is? Simple models allow us not only to disprove hypotheses, but also to explore other possibilities. The simplicity and speed of the box model allowed extensive sensitivity studies (Li et al. 2000) which revealed that large ecosystem changes *can* be induced by relatively small changes in the biological rate parameters, specifically phytoplankton growth rate, zooplankton growth rate, and zooplankton mortality rate. The latter is arguably the most poorly known of the three, including as it does effects of predation losses as well as natural mortality. Figure 8 illustrates the effects of allowing stochastic variation of zooplankton mortality rate (see Appendix B) in a multiyear simulation with fixed physical forcing, hence a constant annual cycle of all physical variables. The biological fields now exhibit greatly increased interannual variability, particularly pronounced in the Strait of Georgia, where there are many "normal" years with spring peaks of phytoplankton and zooplankton but also a year (asterisk) of large phytoplankton standing stocks (and almost no zooplankton) throughout the lighted seasons of the year, followed immediately by a year in which the spring bloom of phytoplankton is greatly reduced in both magnitude and extent but zooplankton biomass is not obviously different from normal.

When trying to decide whether Fig. 8 exhibits perhaps too much interannual variability, we begin to appreciate the dearth of observational data with which to validate biological model results, whether they come from simple and cheap box models like the present one or from much more complex and expensive models with high spatial resolution and more "realistic" biology. In the entire GHF system, there are very few measurements of annual cycles of nitrate, fewer such measurements of phytoplankton and (or) zooplankton biomass, and even fewer measurements of the interannual variability of these quantities. For the GHF system, there are only fragments of the kind of data needed for model validation. However, the existing fragments suggest that the interannual biological variability produced by this simple model is reasonable in both character and magnitude. Figure 9 shows two consecutive years of monthly phytoplankton and zooplankton measurements taken by Stockner et al. (1979) at a grid of stations in the southern Strait of Georgia. In spring 1975, both phytoplankton and zooplankton standing stocks are strongly peaked, a "normal" seasonal cycle for the Strait of Georgia (Fig. 6). However, in the very next year, phytoplankton stocks are significantly larger and remain at these levels throughout the lighted season, while zooplankton standing stock is low. Similar behaviors have already been pointed out in the simulation results shown in Fig. 8.

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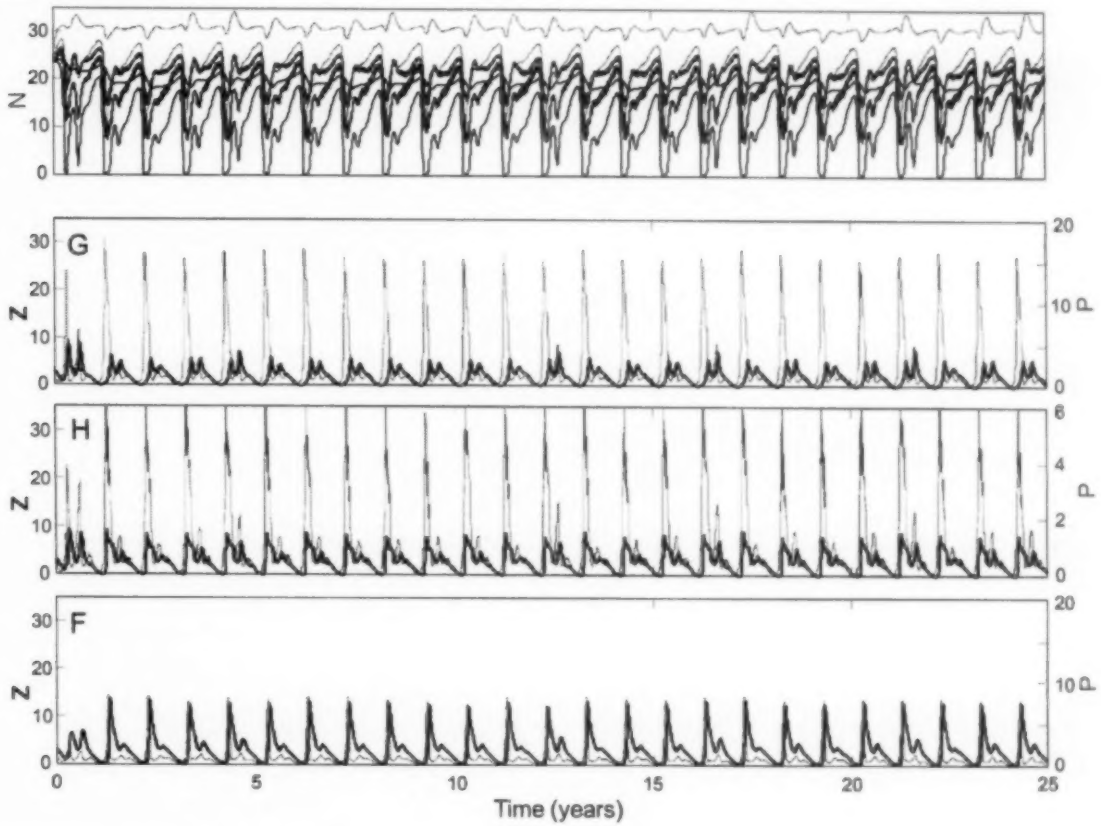
Fig. 7. Biological time series resulting from the 25-year model run with stochastic physical forcing shown in Fig. 5 and constant biological parameters. Line width conventions are the same as in Fig. 5; abbreviations are the same as in Fig. 6. All variables are in nitrate units of mmol $NO_3 \cdot m^{-3}$.



Investigation of the GHF biological–physical system, as represented by our box model, leads us to conclude that in a strongly estuarine system, reasonable variability in physical forcing will not translate directly into large changes in zooplankton standing stocks and hence cannot be a *direct* cause of large variation in juvenile salmon survival based on food availability. However, small changes in poorly known biological rate parameters can produce large interannual variations in zooplankton standing stock, variations consistent in both pattern and levels with available observational data in the Strait of Georgia. Thus, if the physical environment *does* produce a significant effect on the output of the biological system in the Strait of Georgia, it apparently does so only indirectly, through effect(s) of physical processes on biological rate parameters.

One obvious way in which estuarine physical processes can affect biological rate parameters is through the silt content of freshwater forcing, itself linked to atmospheric forcing on both interannual and decadal time scales. As illustrated in Fig. 10 for the Fraser River, suspended sediment transport typically varies strongly with river flow, whether measured by annual peak or annual mean values. Thus, in years of stronger than average freshwater input to catchment areas, river plumes entering estuarine regions not only cover larger areas, but also carry higher suspended loads. Such suspended material will arguably influence all three of the fundamental growth rates involved in zooplankton production. Suspended sediment will affect the light environment in which phytoplankton grow, thus affecting the phytoplankton growth rate. Because zooplankton mechanically sense and capture their prey, an increased percentage of nonfood (sediment) particles in their environment should decrease zooplankton growth rate. However, poorer zooplankton growth may be partially or completely offset by decreased predation losses (zooplankton mortality rate), as higher sediment concentration degrades the visual environment in which larval fish search for and capture their prey. Which of these diverse impacts will dominate change in productivity of a highly nonlinear marine ecosystem is an important question for future investigation.

Discussion

This paper has considered various methods for testing the optimal stability window (Gargett 1997) as a mechanistic underpinning for observed correlations between North Pacific salmon catch and variation in atmospheric forcing of the ocean. We first considered the use of retrospective analyses of historical in-water data to establish a connection between water column stability and marine survival of salmon.

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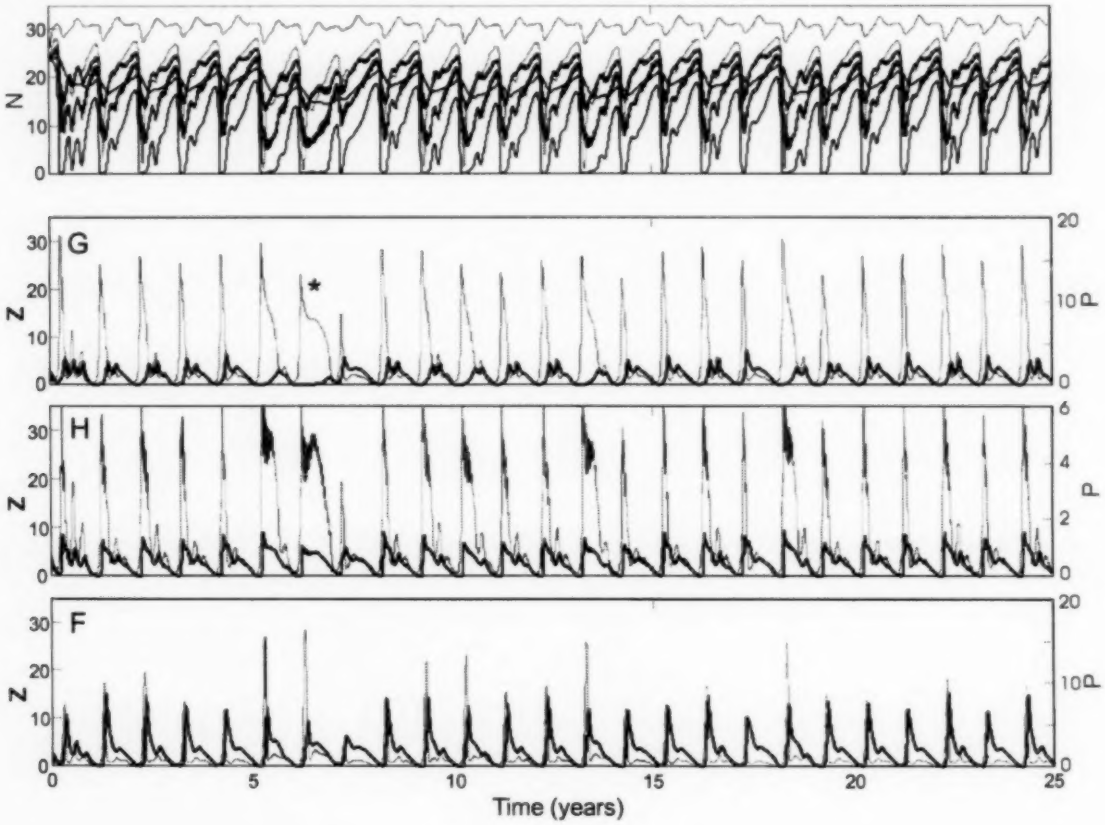
Fig. 8. Biological time series resulting from a 25-year model run with constant annual cycle of physical forcing (identical annual cycles of physical variables) and stochastic variation of zooplankton mortality rate. Line width conventions are the same as in Fig. 5; abbreviations are the same as in Fig. 6. All variables are in nitrate units of mmol $NO_3 \cdot m^{-3}$.



Results from a coastal area off the west coast of Vancouver Island suggest that that this outer coastal region acts as a northern regime, with an optimal window in stability centered around ~0.03 $k \cdot m^{-3} \cdot m^{-1}$. When stability is near this value, during the late 1930s and the 1980s, northern stocks on average produced large catches. Northern catches were low during periods when stability fell below this level, e.g., during the 1960s, or substantially exceeded it, e.g., 1959–1960. While this analysis is suggestive, problems of data density in both time and space made it difficult to form reliable time series of water column stability over the required decadal time scales, even in the "well-sampled" region examined. Continuously sampled time series of temperature and (or) salinity at various shore stations are a potential source of longer surrogate records of stability for use in testing the window hypothesis but prove unsatisfactory for two reasons. First, the necessary assumption of constant lower layer properties is unfounded, at least in the British Columbia coastal area that we have examined. Second, it could become necessary to use a surrogate for a surrogate in northern regions, where density is dominated by salinity but long time series of surface salinity are rarely available. (Dis)proof of the stability window mechanism from observed water column properties awaits establishment and maintenance of repeat CTD stations in the coastal ocean at the northern and southern limits of the range of North Pacific salmonids and another full "cycle" of decadal variation in atmospheric forcing.

In the meantime, even very simple models of the biological–physical system in smaller domains may provide important tests of the optimal window hypothesis; in the region that we modelled, it failed. Nonetheless, the focused process of attempting to test the hypothesis provided a framework for understanding why it failed (because the strongly estuarine physics of the modelled system differed significantly from the physics underlying the original window hypothesis). The model developed in the process of testing also provided a tool for exploring other mechanisms by which the physical ocean environment, itself forced by the atmosphere, could affect marine productivity. We suggest that in strongly estuarine environments such as the Strait of Georgia, variability in atmospheric delivery of freshwater to the estuarine catchment area could cause associated variability in marine primary and secondary productivity through effects of silt content on biological rate parameters. Because the zooplankton production that supports marine fisheries depends on both phytoplankton and zooplankton rate parameters, the phase of any relationship between freshwater input and pro-

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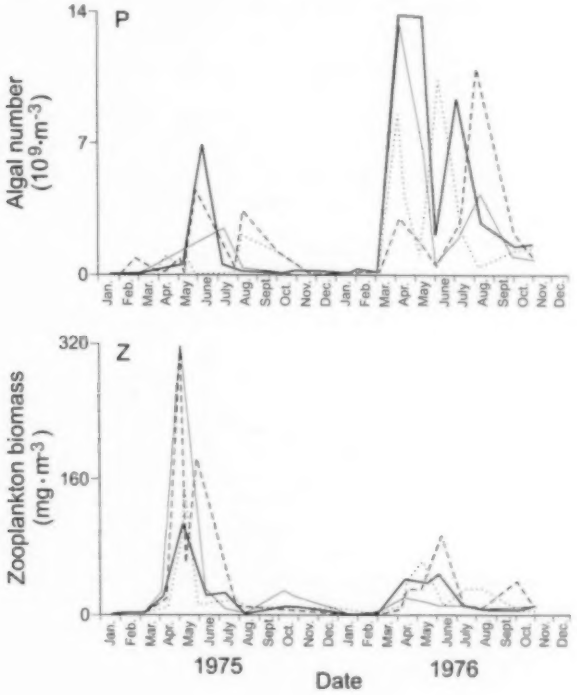
Fig. 9. Strong interannual variability, similar to that observed in model runs with stochastic zooplankton mortality rates (cf. Fig. 8), is seen in two consecutive years of phytoplankton (P) and zooplankton (Z) observations taken monthly over a grid of stations in the southern Strait of Georgia (Stockner et al. 1979). Stations: 5, heavy solid line; 6, light solid line; 7, dotted line; 8, broken line.



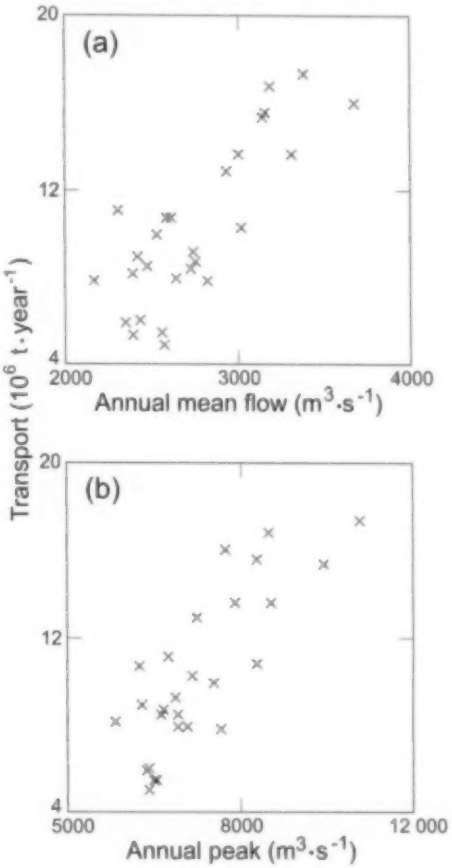
ductivity will depend on the net result of these indirect effects of the physical environment on all relevant rate parameters.

The results of this attempt to test the optimal window hypothesis are mixed. On the outer coast of southern Vancouver Island, available historical data appear at least consistent with an assumption that this region acts as a northern regime with maximum production of salmon occurring within an optimal range of water column stability. In contrast, a model of the Strait of Georgia shows that the biological productivity of this region is not determined by the physical processes assumed to underlie the optimal window hypothesis. On the basis of these results, we suggest that the optimal window hypothesis will be applicable as a predictive tool in areas where juvenile salmon enter the coastal ocean directly but inapplicable in other regions where they spend the first few to several weeks of their ocean lives in a strongly estuarine environment.

Acknowledgments

We thank Ron Perkin for maintaining the British lighthouse data, Skip McKinnell for accessing the Chilko Lake time series, and Ken Denman for his contribution to the GHF box model.

Fig. 10. Variation of the suspended sediment (clay plus silt) load carried into the Strait of Georgia by the Fraser River as a function of (*a*) mean annual flow and (*b*) annual peak flow (sediment data, 1966–1992, courtesy of M. Church, Geography Department, University of British Columbia, Vancouver, B.C.).



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Appendix A. Stochastic variability of physical forcing of the GHF box model

Fraser River freshwater input to the Strait of Georgia model is represented by the functional form freshwater flow (FF) (cubic metres per second)

$$\mathrm{FF}(t) = F_w + F_f \ \mathrm{sech}^2\left(\frac{t - t_p}{t_w}\right)$$

where winter flow $F_w = 10^3$ m^3·s^{-1} is constant and F_f is the peak of freshet flow above F_w, t_p is the time of peak freshet flow, and t_w is its time extent; all are considered stochastic variables of the generic description

$$v = v_o + v_r \ \mathrm{svar}$$

where svar is a random variable uniformly distributed in [0,1]. Table A1 shows values of v_o and v_r for the three variables, chosen from historical records of Fraser River flow. The functional form FF(t) is multiplied by a factor of 1.5 (Griffin and LeBlond 1990) to allow for covarying flow of other rivers and streams into the Strait of Georgia.

Table A1. Offset (v_o) and range (v_r) values for the stochastic model parameters describing interannual variability in physical forcing.

	v_o	v_r
F_f (m^3·s^{-1})	3×10^3	8×10^3
t_p (months)	5	1
t_w (months)	3	1
S_u	0	2
t_{lag} (months)	0	2

The second forcing function, that of the "deep Pacific salinity" towards which the salinity of the deep F box is continuously restored, represents an annual cycle imposed by summer upwelling of high-salinity California Undercurrent water:

$$\mathrm{SP}(t) = S_w + S_u \mathrm{sech}^2\left(\frac{t - t_p - t_{lag}}{t_u}\right)$$

where base (winter) salinity S_w = 32.5 and time extent t_u = 3 months of the upwelling period are fixed but S_u, the maximum salinity increase associated with upwelling, and t_{lag}, the time lag between the time t_p of Fraser freshet peak (itself a stochastic variable, see above), are stochastic variables. Values in Table A1, resulting in maximum (summer) values between 32.5 and 34.5, were based on a compilation of historical salinity data for the "deep" (depth >50 m) Juan de Fuca Strait (W.R. Crawford, Institute of Ocean Sciences, Sidney, B.C., personal communication). Because water upwelled in summer is high in nutrients as well as salinity, the model also restores the nitrate of the deep Juan de Fuca box to a seasonally varying function derived from the above salinity function and the deep nitrate–salinity correlation shown by Mackas and Harrison (1997, their fig. 6*a*).

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Appendix B. Distribution function for stochastic zooplankton mortality rate

In model runs with stochastic variation of zooplankton mortality rate (z_m), individual values are specified by z_m = (svar)z_{mo}, where z_{mo} is a constant and svar is a stochastic variable. Since biological rates are positive definite, appropriate stochastic values must be chosen from a single-sided distribution function. To generate such a distribution function, we use a normal distribution with mean m_n = 1 and standard deviation σ_n = 1.5. Individual values z_m chosen from this parent population (as returned by the MATLAB random number generator *randn*) are *discarded* unless the mortality rate is both positive and larger than the realized growth rate (while the mortality rate may temporarily exceed achieved growth, it cannot do so on average). Accepted val-

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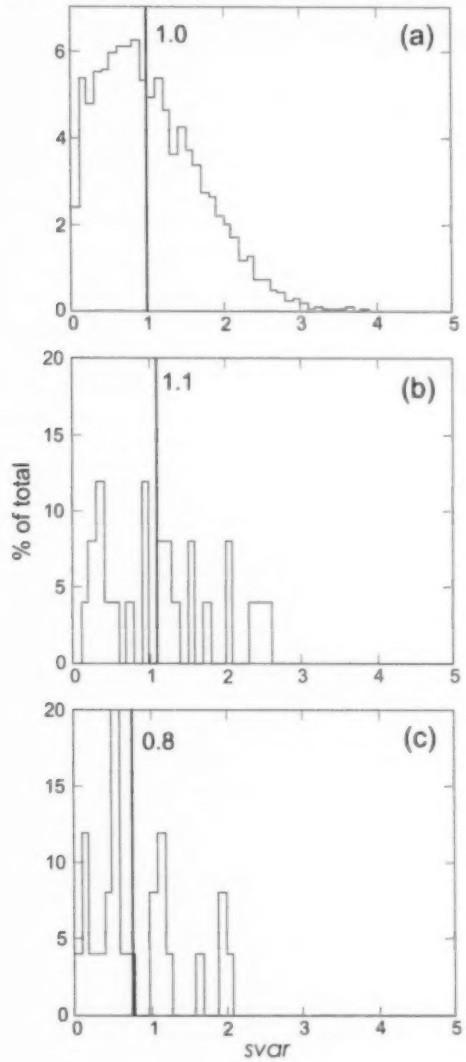
Fig. B1. (*a*) "Discarded normal" distribution suitable for generating (positive definite) biological rates. The large-sample (5000-point) mean has been normalized to 1.0. (*b*) and (*c*) Consecutive 25-point samples chosen from the discarded normal distribution illustrate the well-known fact that small-sample (25-point) means may differ substantially from both the large-sample mean and each other.



ues form the "discarded normal" distribution seen in Fig. B1*a* normalized to a large-sample mean of 1.0. While other positive definite distributions may be generated, the discarded normal distribution seems a reasonable (perhaps conservative) first-order description of variability in the underlying mortality rate.

It should be noted that means over small samples (such as the 25 values used in the "long" 25-year runs considered in this paper) may differ considerably from the large-sample mean of $1.0z_{mo}$. Consecutive selection of two 25-value sets (Figs. B1*b* and B1*c*) yielded means of roughly $1.1z_{mo}$ and $0.8z_{mo}$, the latter equal to the small-sample mean for the run shown in Fig. 9. Much larger deviations are possible.

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PERSPECTIVE

Winberg revisited: convergence of routine metabolism in larval and juvenile fish

Alexander B. Bochdansky and William C. Leggett

Abstract: We examined whether Winberg's concept of a single general model describing the relationship between mass and respiration rate in fish can be reliably extended to include larval stages (<1 mg dry weight) that were not assessed in his original analysis. To address this question, we developed an independent data set consisting of 42 sets and incorporating 25 species. Sensitivity analysis (Monte Carlo simulation) verified that the number of data sets used was more than sufficient to establish a general equation of the form sought. The resulting model converged with extrapolation of Winberg's model to the size range of interest and to extrapolation of the Clarke and Johnston model, which, like Winberg's, was restricted to postlarval fish. Thus, the generalization sought by Winberg exists. A single general model derived from first principles of the form

$$\log R = \log\left(\frac{1}{\frac{1}{10^{(-3.71+\log dw)}} + \frac{1}{10^{(-2.40+0.67\log dw)}}}\right)$$

reliably describes the relationship between respiration rate and mass for fishes over the size range 1–10^8 µg dry weight. The curvilinearity of this model reflects the reality that the mass exponent in the relationship between body size and respiration rate decreases during ontogeny.

Résumé : Selon Winberg, il existe un modèle général unique qui décrit la relation entre la masse et le taux de respiration chez les poissons. Nous avons regardé si le modèle pouvait être étendu afin de tenir compte des larves de poissons non incluses dans l'analyse originale. Pour ce faire, nous avons monté une banque de données indépendantes composée de 42 séries de mesures sur 25 espèces. Une analyse de sensibilité (simulation de Monte Carlo) a permis de vérifier si le nombre de séries de données que nous avons utilisé était suffisant pour établir une équation du type requis. Le modèle obtenu convergeait avec l'extrapolation du modèle de Winberg pour les tailles visées et celle du modèle de Clarke et Johnston, les deux modèles ayant été développés pour des poissons qui ont terminé leur vie larvaire. La généralisation recherchée par Winberg existe donc. Un modèle général unique dérivé des principes premiers de la forme

$$\log R = \log\left(\frac{1}{\frac{1}{10^{(-3.71+\log dw)}} + \frac{1}{10^{(-2.40+0.67\log dw)}}}\right)$$

décrit efficacement la relation qui existe entre le taux de respiration et la masse chez les poissons dont la masse sèche varie entre 1 à 10^8 µg. La curvilinéarité du modèle souligne le fait que l'exposant de la masse dans la relation entre la taille du corps et le taux de respiration décline durant l'ontogenèse.

[Traduit par la Rédaction]

Introduction

The Russian scientist Winberg (1960) collected and analyzed data on the routine metabolism of juvenile and adult fish from the literature and concluded, "[...] there is no need for additional accumulation of data on the metabolic rate of fish under conditions of weak activity or nearly resting, because not one of the basic problems of theoretical or practical interest, for which fish respiration is measured, can be solved in that manner." The general equation for routine me-

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tabolism corrected to a temperature of 20°C (table of multipliers in Winberg 1960; Krogh 1916) was

$$(1) \qquad R_W = 0.307\, W_W^{0.81}$$

where R_W is oxygen consumption (millilitres per hour) at 20°C and W_W is the wet weight of the fish (grams). Winberg (1960) concluded that this general equation adequately describes the routine metabolism of fish irrespective of taxonomic position or habitat (marine or freshwater). Without reference to Winberg (1960), Clarke and Johnston (1999) performed a similar analysis and concluded that the general equation linking oxygen consumption to body weight has the form

$$(2) \qquad R_{C\&J} = 0.0044\, W_{C\&J}^{0.80}$$

where $R_{C\&J}$ is oxygen consumption (millimoles per hour) and $W_{C\&J}$ is wet weight (grams). Both Winberg (1960) and Clarke and Johnston (1999) excluded data on larval fish from their analyses.

Recent improvements in the methodology of respiration measurement have yielded an abundance of respiration rate estimates for larval fish. Post and Lee (1996) recently reviewed these data. The regression means of larval and juvenile metabolism reported in 83 studies differed by more than 1000-fold, which left little hope that a general equation would be applicable to respiration rates in larval and juvenile fish.

In this study, we reexamine the relationship between metabolism and body weight drawing on pooled data from the literature on larval and juvenile fish and encompassing a wide range of species. Our objective was to explore the distribution and sources of variability in these data, to identify outliers and the factors influencing their deviations, and to compare and contrast the findings of Clarke and Johnston (1999) with our data to evaluate the applicability of a single general equation describing the relationship between metabolism and mass across all developmental stages from larvae to adults.

Materials and methods

We digitized previously published data from figures using Data Thief image analysis software (K. Huyser and J. van der Laan, National Institute for Nuclear Physics and High Energy Physics, Amsterdam, The Netherlands). We recalculated regression parameters for each digitized data set and validated the result by comparison with those reported in the original publications. While considerable overlap exists in the data included in our analysis and those incorporated in reviews by Houde (1989) and Post and Lee (1996), we were more conservative in our use of data. We applied the following three a priori selection criteria in determining the data sets to be included. (*i*) We incorporated only those studies in which the original data reflecting the relationship between oxygen consumption and body weight were presented in a figure. We excluded studies that reported mean values or regression equations. This ensured that the full range of variance within and among data sets was retained in our data. (*ii*) We used only those studies in which oxygen consumption was measured directly. Studies in which oxygen consumption estimates were derived from models or via indirect calculations (gill area, etc.) were excluded. (*iii*) Only those studies that reported at least nine independent measures of respiration were included. This is an arbitrary limit. Very few studies report fewer than nine data points in a regression of respiration against body weight. Most studies with fewer than nine data reported means and were already excluded through the application of the first criterion.

We defined an individual data set as a set unique with respect to author, species, or temperature. Thus, a study by a single author reporting respiration rates for a single species at three temperatures would yield three individual data sets. All data were pooled irrespective of author, taxonomic group, or temperature. Species, author, taxonomic affiliation, and environmental variables were then used as independent variables in statistical models. A general linear model was initially employed to explore the distribution of variances and the significance of various interaction terms. The assumption of linearity is, however, questionable in some comparisons. For example, when log transforming oxygen consumption and body weight, a linear relationship represents a reasonable approximation, but it is not exact (see below). We therefore fit a curvilinear model to the relationship between respiration and body weight employing the Gauss–Newton algorithm. We then used the parameter estimates of the nonlinear model to explore the influence of "investigator bias" on the general equation. We gave particular attention to the weight range below 1 mg dry weight, which was poorly represented in the studies by Winberg (1960) and Clarke and Johnston (1999). All statistical analyses and simulations were performed with SAS statistical software.

All data employed in our analyses were transformed into common units by means of standard conversions. Respiration rates were represented as millilitres of oxygen consumption per day and body weight was expressed as micrograms dry weight. The following conversions were applied. Wet weight was divided by 6 to obtain dry weight (Post and Lee 1996); the protein weight to dry weight ratio was assumed to be 0.5 (Weltzien et al. 1999). We used data from two studies (Kiørboe et al. 1987; Wells and Pinder 1996) that reported standard metabolism. These values were multiplied by 2 to obtain routine metabolism (DeSilva and Tytler 1973). Respiration and dry weight values were either $\log_{10}$ or ln transformed. The ln transformation was used initially, consistent with the convention of incorporating temperature in an "e^{kT}" term, where k is a constant and T is temperature (degrees Celsius). The $\log_{10}$ transformation was employed in figures and in the final equations for ease of display. We extracted 42 data sets from 21 studies involving 25 species (Table 1). The size of individuals represented in the data ranged from 7.8 µg to 50 g. Temperatures at which the metabolic determinations were made ranged from –1.5 to +28°C.

Results and discussion

The complete $\log_{10}$-transformed data set is presented in Fig. 1*a*. The scatter in the original data is restricted to approximately one order of magnitude about the mean. Elimination of data derived from two authors (Laurence 1978; Holeton 1973, 1974) caused the data to converge significantly (Fig. 1*b*). Particularly, the range of respiration rates reported for cod and haddock in Laurence (1978) exceeded the range for all other species combined and therefore considerably contributed to the variance in the larval size range. Holeton's (1973, 1974) high-latitude fish will be examined in more detail below. The large variance found within several studies demonstrates the importance of resting the analysis on individual data rather than on regression means. However, since there was no a priori basis for excluding any of the outlier data sets, all data were retained in the analysis.

When using the linear model approach, all data were pooled and body weight, authors, species, and temperature were used as explanatory variables. The general linear model facilitates partitioning of the explained variance (r^2 in percentage of total variance) among variables:

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Table 1. List of studies.

Study	Species	Temperature (°C)	*n* data points
Cetta and Capuzzo 1982	*Pleuronectes americanus*[a]	7	48
Edwards et al. 1969	*Pleuronectes platessa, Limanda limanda*	10	67
Giguère et al. 1988	*Scomber scombrus*	13–19	121
Holeton 1973	*Salvelinus alpinus*	2, 6	145
Holeton 1974	*Boreogadus saida, Gymnelus viridis*	–1.5	38
Houde and Schekter 1983	*Anchoa mitchilli, Archosargus rhomboidalis, Achirus lineatus*	26, 28	34
Kamler et al. 1987	*Cyprinus carpio*	26	109
Keckeis and Schiemer 1990	*Alburnus alburnus, Rutilus rutilus*	20	77
Keckeis and Schiemer 1992	*Rutilus rutilus, Abramis ballerus, Alburnus alburnus*	20	48
Kiørboe et al. 1987	*Clupea harengus*	8	87
Kudrinskaya 1969	*Stizostedion lucioperca, Perca fluviatilis, Abramis brama, Rutilus rutilus*	20	138
Laurence 1978	*Gadus morhua, Melanogrammus aeglefinus*	7–10	150
Mishra and Singh 1979	*Anabas testudineus*	28	45
Mukhamedova 1977	*Hypophthalmichthys molitrix*	20	168
Oikawa and Itazawa 1995	*Cyprinus carpio*	25	45
Oikawa et al. 1991	*Pagrus major*	20	36
Quantz and Tandler 1984	*Sparus aurata*	19, 24	44
Sheel and Singh 1981	*Heteropneustes fossilis*	28	28
Singh et al. 1982	*Channa punctatus*	28	39
Torres et al. 1996	*Sciaenops ocellatus*	24	48
Wells and Pinder 1996	*Salmo salar*	10	47
Wieser and Medgyesy 1990	*Rutilus rutilus*	15, 20	22

[a]Previously *Pseudopleuronectes americanus*.

$$(3)\quad \ln R = \underset{92\%}{\beta_0} + \underset{5.6\%}{\beta_1 \ln \mathrm{dw}} + \underset{0.14\%}{\beta_2 \mathrm{sp}} + \underset{0.1\%}{\beta_3 \mathrm{au}} + \beta_4 \mathrm{temp} + \underset{0.086\%}{\mathrm{interaction\ (sp \times temp)}} + \underset{2.1\%}{\varepsilon}$$

where dw is the dry weight (ratio variable), sp is the species (categorical variable), au is the author (categorical), temp is the temperature (ratio), and ε the error term or residual variance. All components in eq. 3 were significant at $p < 0.0001$ ($n = 1584$). The interaction between species and temperature was significant but explained only 0.1% of the variance. If one assumes no author or species effects, the variance component can be interpreted as being predominantly attributable to temperature. However, even in this extreme case, temperature explained only 1.4% of the variance (eq. 4):

$$(4)\quad \ln R = \underset{92\%}{\beta_0} + \underset{1.4\%}{\beta_1 \ln \mathrm{dw}} + \underset{6.6\%}{\beta_2 \mathrm{temp}} + \varepsilon$$

We conclude that eq. 3 reflects a more realistic distribution of variances. Hence, approximately 6% of the variance in respiration rates was attributable to author and species effects. The small amount of variance explained by temperature as shown by eqs. 3 and 4 does not imply that temperature is unimportant for the metabolism within species. Rather, it shows that temperature can be ignored when defining the relationship between metabolism and mass across species and a wide size range (i.e., very little noise is attributable to a temperature effect).

Allometry

As previously noted, the assumption of linearity is not uniformly valid. In fact, the relationship between log[dry weight] and log[respiration] has repeatedly been shown to be nonlinear and is often described as biphasic and triphasic (summarized in Oikawa et al. 1991; Post and Lee 1996). This implies that the mass exponent is not invariant as might be inferred from Peters' (1983) general "mouse–elephant" curve. Larval fish scale isometrically with an exponent of 1, while juvenile and adults scale with exponents close to 0.8 (Giguère et al. 1988). The key to this variance appears to be body size rather than developmental stage. Rombough and Moroz (1997) and Hughes and Al-Kadhomiy (1988) have effectively refuted the suggestion that scaling changes with the development of gills and the diffusion processes across surfaces. Others have invoked metamorphosis from the larval to juvenile stage (Wells and Pinder 1996) and (or) development of the circulatory system (Goolish 1995) to account for the changing mass exponent. However, changing mass exponents during ontogeny are not restricted to fish and have been well documented in many other small organisms including invertebrates and developing mammals (Wieser 1984). To date, there is no satisfactory explanation of the reality that the metabolic exponent exhibits values close to 1 in small organisms (millimeters and micrograms) and stabilizes between 0.7 and 0.8 in larger organisms.

Recognizing the slight curvature reflected in the data in Fig. 1, we fit the simple empirical model (Fig. 2)

$$(5)\quad \ln R = A + B\,(\ln \mathrm{dw})^C$$

Equation 5 was fit using the Gauss–Newton method in the NLIN procedure of SAS. The resulting model was

$$(6)\quad \ln R\ (\mathrm{mL \cdot day^{-1}}) = -12.03 + 3.27\ [\ln \mathrm{dw}\ (\mu\mathrm{g})]^{0.57}$$

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Fig. 1. Relationship between fish metabolism and mass derived from (*a*) 42 data sets and (*b*) all data except those by Laurence (1978) and Holeton (1973, 1974).

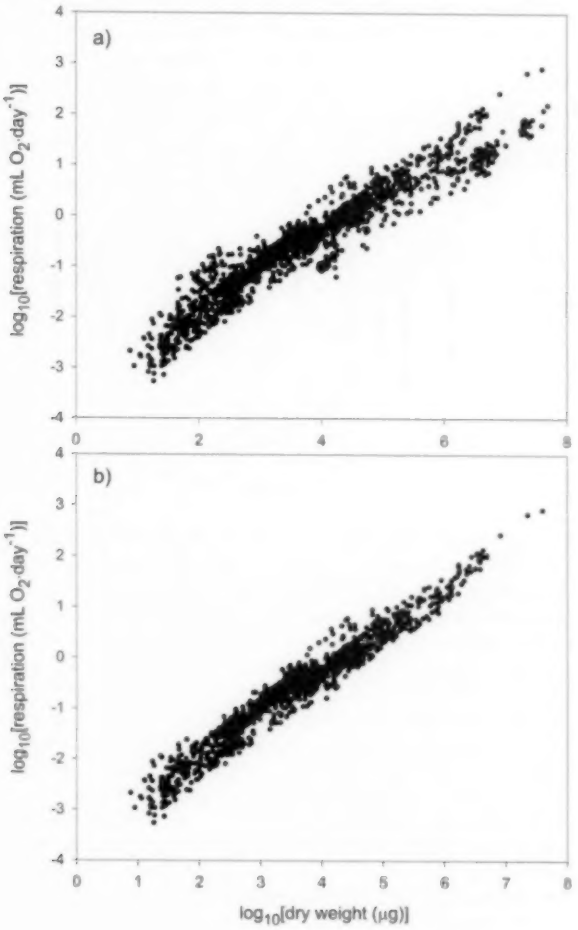


Fig. 2. Fit of the curvilinear model $\ln R = A + B \log dw^C$ (eq. 5) to the complete data set, where R is respiration rate (mL·day^{-1}), dw is dry weight (µg), and A, B, and C are parameters. The numbers indicate values of the continuously changing mass exponent at five points along the curve. Model: $R = -12.03 + 3.27\ [\ln dw\ (mg)]^{0.57}$.

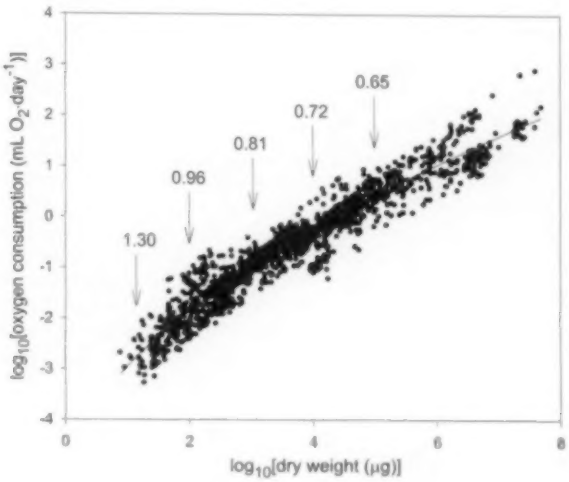
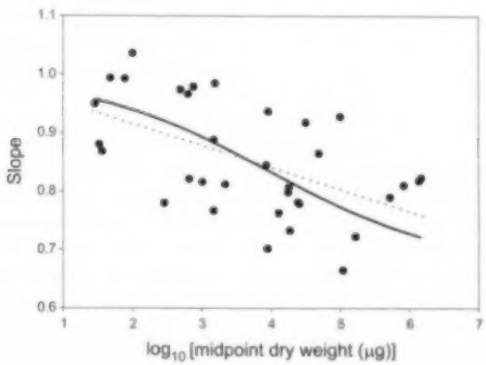


Fig. 3. Plot of mass exponent (slope) for individual regressions against the midpoint of dry weight of each regression. Seven data points have been removed by Cook's D and the "mean shift outlier" procedure to yield more robust parameter estimates (Myers 1990). Linear regression (dotted line): slope = 0.99 – 0.038 log dw. The solid line represents the fitted eq. 13 (first derivative of eq. 12).



The nonlinearity of the relationship between respiration versus mass is reflected in the exponent $c < 1$. The allometric exponent of respiration on mass at each weight is the slope of the tangent to the curve (i.e., the first derivative of eq. 6). Figure 2 displays the slope of tangents at five points along the curve. The slope of eq. 6 changes from 1.3 at 10 µg to 0.65 at 100 mg. The problem in using the above approach is that the position of individual outlier data sets could strongly influence the curvature of the overall regression. To avoid this problem, we chose to plot the slopes of individual data sets against the mean of their dry weights (Fig. 3). This is a more conservative procedure, since the slopes of the individual regressions themselves represent a mean of each data set. There is, therefore, little danger that outliers in the original data could exert a strong influence on outcome of the analysis. In addition, we employed Cook's D and the "mean shift outlier" procedure (Myers 1990), which provided more robust parameter estimates (Fig. 3). The resulting slope approximates 1 for animals of approximately 10 µg in weight and declines to approximately 0.75 for animals averaging 1 g. A fundamental discrepancy exists between the output of the analyses in eq. 6 and Fig. 3. In particular, the exponent changes more drastically under the conditions specified in eq. 6. Specifically, the nonlinear eq. 6 suggests an exponent of 0.65 at 100 mg compared with a value of 0.8 derived from the linear relationship in Fig. 3 at the same weight. The curvature in Fig. 2 appears to be exaggerated relative to the rate of change derived from the more conservative approach reflected in Fig. 3. The overriding conclusion, however, is that there is no strong transition point in the allometric relationship. Rather, the exponent appears to decrease gradually and continuously.

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Fig. 4. Krogh's multiplier to correct respiration rates to 20°C (individual points from table 1 in Winberg 1960) (circles), and the multiplier derived from the Arrhenius equation (Clarke and Johnston 1999; ln[multiplier] = 1.2 – 0.06 temperature (°C)) (solid line).

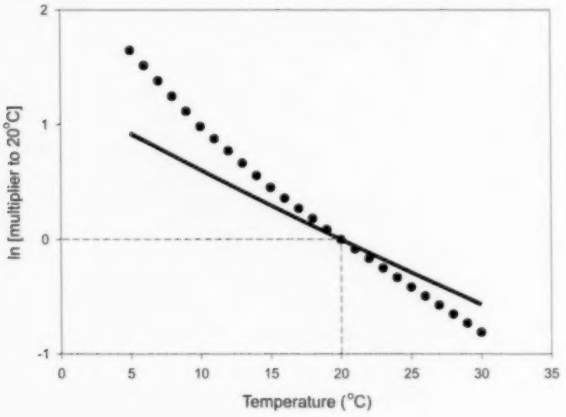
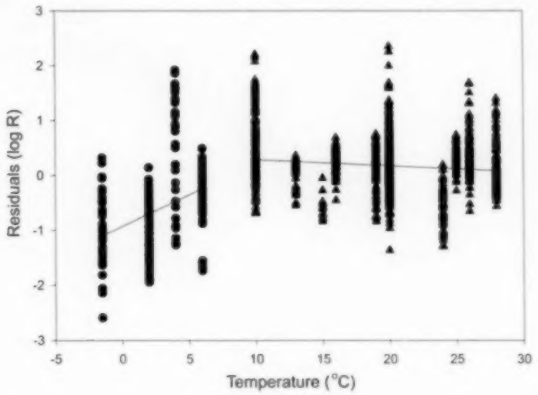


Fig. 5. Relationship between residuals (derived by fitting eq. 5 to the complete data series) and temperature. Between 4 and 28°C, there was no discernable effect of temperature. Temperature had a significant effect between –1.5 and 6°C. Equation of the linear regression at temperatures between –1.5 and 6°C: residuals = –0.928 + 0.115 temperature (°C) (r^2 = 0.119, p < 0.0001, n = 216).



Effect of temperature

Winberg (1960) accommodated temperature effects by standardizing all data to 20°C using the "normal curve" (Krogh 1916). After carefully examining temperature relationships in various temperate fishes, he concluded that Krogh's normal curve yielded results with "sufficient accuracy." However, he acknowledged Scholander et al.'s (1953) data, which suggested that Arctic fish have elevated metabolic rates relative to tropical fish at the same temperature and concluded that in this special case, the normal curve would underestimate oxygen consumption rates. Wohlschlag's (1960) data supported Scholander et al.'s (1953) hypothesis, and the idea of metabolic cold adaptation became dogma.

While some physiologists continue to search for explanations for metabolic cold adaptation at the cellular and enzymatic level, evidence is mounting that the phenomenon does not exist. Holeton (1974) was one of the first to criticize Scholander et al.'s (1953) and Wohlschlag's (1960) theory. He argued that the apparent cold adaptation, and hence increased metabolic rate, in high-latitude fish was an artifact created by handling stress. He noted that the metabolism of Arctic fish kept in the respiration chambers for long periods dropped to more normal levels. Clarke and Johnston (1999) found no evidence of metabolic cold adaptation in an intercomparative analysis of 69 species drawn from 28 families and 12 orders. Clarke (1991) has questioned the metabolic approach to study cold adaptation, noting that there is no a priori reason why any poikilothermic animal should adjust its metabolic rate to temperature, the response of metabolic rates being multicausal and indirect, reflecting the interplay of growth, activity, feeding, reproduction, and survival at variable and varying temperatures.

This having been said, a general correction for temperature is likely to be judicious when comparing data derived from organisms occupying different temperature regimes if only due to acclimation effects. For postlarval fish, Clarke and Johnston (1999) advocated an equation attributed to Arrhenius that employs the inverse of temperature to linearize the relationship between metabolism and temperature. Their cross-species analysis indicated the slope of the relationship between metabolism and temperature to be considerably shallower than expected from the Krogh normal model (Fig. 4). Rombough (1988) reported a stronger temperature dependence of oxygen consumption by fish eggs and larvae. In this study, metabolic rates approximately tripled as temperatures increased from 10 to 20°C, and as with Krogh's normal curve, the metabolic rates increased by an order of magnitude from 4 to 28°C. In another review, Houde (1989) related metabolism to temperature for larvae of 13 fish species. He removed one "outlier" (haddock, Laurence 1978), which yielded a significant relationship (p = 0.031, n = 12). However, this relationship fails if only one additional point (*Archirus lineatus*) is removed (p = 0.138, n = 11; our analysis). The interpretation of the temperature relationship in this example is therefore problematic.

Given the above, we analyzed our data for possible temperature influences on metabolism. To avoid problems associated with calculating weight-specific rates over a wide range of body sizes (Blaxter 1992), we plotted the residuals of the respiration–weight relationship (eq. 6) against temperature (Fig. 5). The magnitude of the differences between the temperature extremes (–1.5 and 28°C) is consistent with that predicted by the Arrhenius equation. However, no temperature effect could be identified over the temperature range 4–28°C (Fig. 5).

Rombough (1988) argued that ambient temperature changes have a more pronounced effect on the early life stages than on later developmental stages due to the higher degree of stenothermy of the former. If true, temperature dependence may be more apparent when smaller sized animals are assessed. To evaluate this possibility, we calculated the means of metabolic rates for animals <1 mg in weight for a grand covariate mean of 158 µg. Within this limited weight range, there was no need to account for the nonlinearity of the allometric relationship. There was no effect of temperature on metabolic rate at >4°C (Fig. 6). Why? We can only

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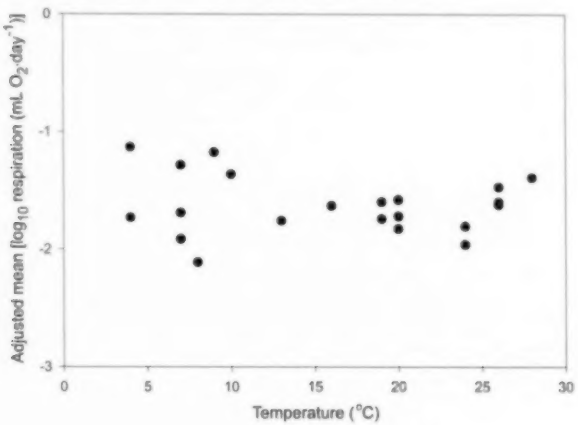
Table 2. Influence of phylogenetic group, order (O), and family (F) on the residuals (res) after fitting oxygen consumption rates against body mass.

Model	*n* groups	Type of test	r^2	*p*
(1) res = $\beta_0 + \beta_1$temp + β_2O + β_3(temp × O) + ε	8	ANOVA	r^2(O) = 0.25	p(O) < 0.0001
(2) res = $\beta_0 + \beta_1$temp + β_2F + β_3(temp × F) + ε	15	ANOVA	r^2(F) = 0.36	p(F) < 0.0001
(3) res = $\beta_0 + \beta$temp + β_1O + β_3(temp × O) + ε	2	ANCOVA	r^2(O) = 0.0004	p(O) = 0.51

Note: r^2 and *p* are the explained variance and the probabilities (that the null hypothesis is correct), respectively, after taking the significant covariate temperature (temp) into account. The first two models are confined by a lack of degrees of freedom on the species level. This means that order–family–species cannot be separated. In the third analysis, the two major orders cypriniformes and perciformes were used. There was no evidence for significant difference between the two orders.

Fig. 6. Adjusted means of oxygen consumption rates of larvae <1 mg relative to incubation temperature. The grand covariate mean for these data sets was 158 µg dry weight.



speculate. In the studies that we examined, metabolic measurements were made allowing ample acclimation time at temperatures close to the species optimum, or well outside any stressful temperature ranges. Is it possible that the sum of all temperature adaptations for growth and activity results in a similar metabolic expenditure? Clearly, temperature plays an important role in the physiology of individual fish. It appears, however, that it has very little influence on estimates of metabolism in larval fish across taxonomic groups. Metabolism as an expenditure term is the result of growth, activity, reproduction, foraging, etc. These performance components are selected for, and not metabolism per se. We therefore essentially share Clarke's (1991) view that the arguments for metabolic temperature adaptations in fish are fundamentally flawed. However, there does appear to be some mechanism at work, which results in increased metabolism at lower temperatures in cold-water species relative to temperate or warmwater species when both are exposed to the same temperatures. This effect is also evident in the relatively shallow slope of the temperature multiplier derived from Clarke and Johnston's (1999) multispecies comparison (Fig. 4).

Effect of phylogenetic grouping

In our data set, the number of cases in which the same species was studied by two or more independent investigators was very small. It was therefore impossible to isolate investigator from species effects. At higher taxonomic levels (families and orders), some separation was possible. We analyzed the residuals of the nonlinear regression of metabolism against body weight (eq. 6) using analysis of covariance with temperature as the covariate. Both family and order contributed significantly (Table 2). It should be noted, however, that the number of species per family/order was limited. Therefore the effect of family/order is strongly influenced by the small number of species within each family/order. Two orders were species rich (cypriniformes, seven species; perciformes, nine species). There was no significant difference in respiration rates between the two orders (p = 0.513, n = 971) when the residuals of eq. 6 were evaluated using temperature as the covariate. Our results are consistent with that of Clarke and Johnston (1999) who reported a significant but weak effect of phylogenetic grouping. This outcome is not surprising given that oxygen consumption is a composite expenditure term reflecting a multitude of adaptations and constraints related to activity, feeding, and reproduction.

How much data is enough?

We performed a sensitivity analysis to assess the impact of sample size on the reliability of the conclusions drawn. We randomly subsampled individual data sets from our total data series to create subsets of the total (i.e., Monte Carlo simulations/bootstrapping). Using the nonlinear expression relating metabolism to body mass (eq. 5), we calculated the parameters *A*, *B*, and *C* based on random subsamples of the original data series. We repeated the procedure 30 times, calculating parameters based on two, three, four through the full 42 data set series. The variance of the parameter estimates so derived decreased with sample size, converging at the 42 data set variance developed in eq. 6 (Fig. 7). Slight asymmetry occurred because of autocorrelation of the three parameters. At sample sizes >30 data sets, there was little or no improvement (75% of the parameter estimates based on n = 30 fall within the 95% confidence limits for the full series) (Fig. 8). We conclude that the 42 data set suite that we assessed was sufficient. Moreover, given that the data derive from multiple laboratories and a variety of analytical techniques, a common bias in the published data is unlikely.

Was the relationship we derived biased by authors?

Extreme values can bias parameter estimates. We tested for this effect by recalculating the parameter values omitting one author at a time from the total series. This analysis paints a "worst-case" scenario, since there is often more than one data set per study. The approach is also consistent with the view that experimental protocols and techniques are

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Fig. 7. Monte Carlo simulation of the influence of sample size on the variability of the parameter estimates of the general model $\ln R = A + B \ln dw^C$ (eq. 5). (*a*) Parameter *A*; (*b*) parameter *B*; (*c*) parameter *C*. Where possible, the procedure was repeated 30 times for a particular sample size.

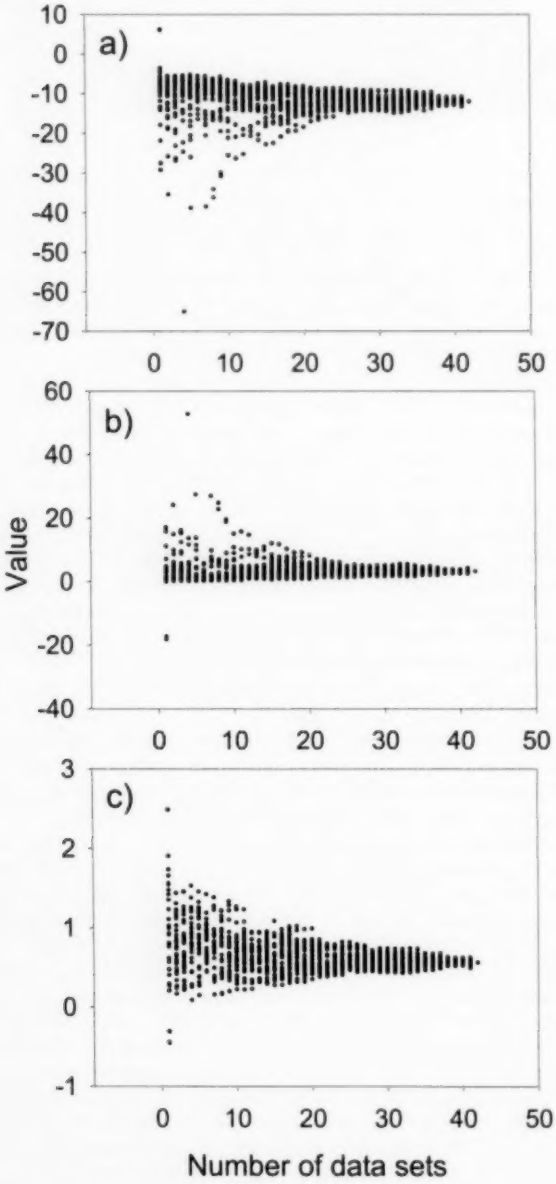
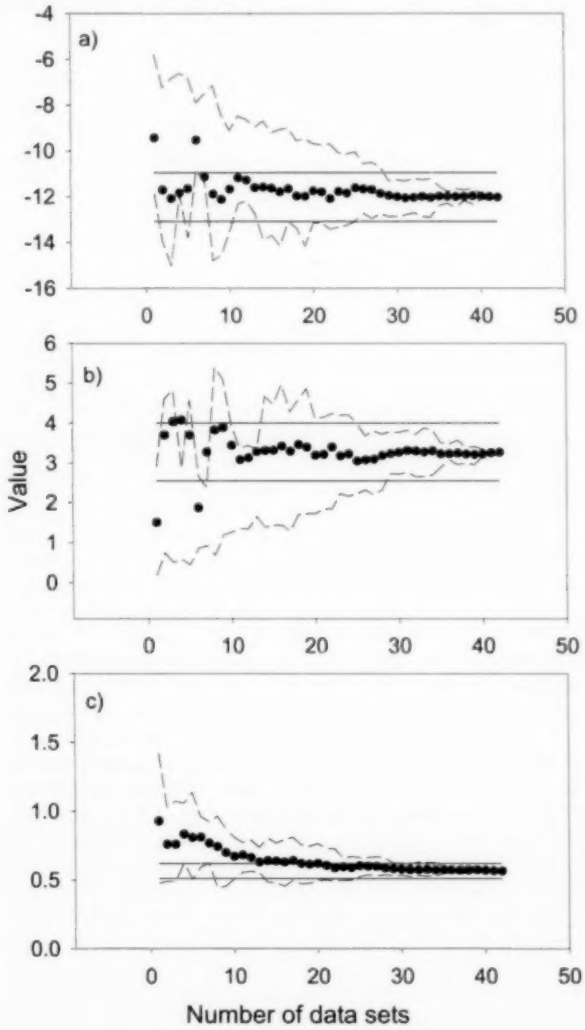


Fig. 8. As in Fig. 7 but showing the quartiles of the parameter estimates at each sample size (broken lines) and the calculated means (circles). For comparison, the 95% confidence limits of the final parameter estimates (based on 42 data sets) have been superimposed (solid lines). At more than 30 data sets, 75% of the parameter estimates fall within the 95% confidence limits. (*a*) Parameter *A*; (*b*) parameter *B*; (*c*) parameter *C*. Estimates using all 42 data sets: $A_{42} = -12.03$ (SE = 0.54), $B_{42} = 3.27$ (SE = 0.37), and $C_{42} = 0.57$ (SE = 0.03).



more consistent within versus between authors. The parameter values derived from each omitted study are presented in Fig. 9. Holeton's (1973, 1974) data on polar fishes exhibit the strongest influence on the final parameter estimates. To investigate the maximum deviation from the mean, we therefore calculated oxygen consumption for the total series with Holeton's (1973, 1974) data excluded (Table 3). Holeton's (1973, 1974) data create a maximum bias in oxygen consumption of approximately 30%. However, by applying an appropriate temperature correction, this bias is eliminated (Fig. 5). We conclude that the parameter estimates are robust.

How do recent data compare with Winberg (1960)?

The data analyzed in this study were all published post-Winberg (1960). They therefore represent a truly independent test of Winberg's (1960) equation. Given that very few data for fish smaller than 1 mg and no data smaller than 100 µg were incorporated into the model developed by Winberg (1960), the smaller size range now available is of

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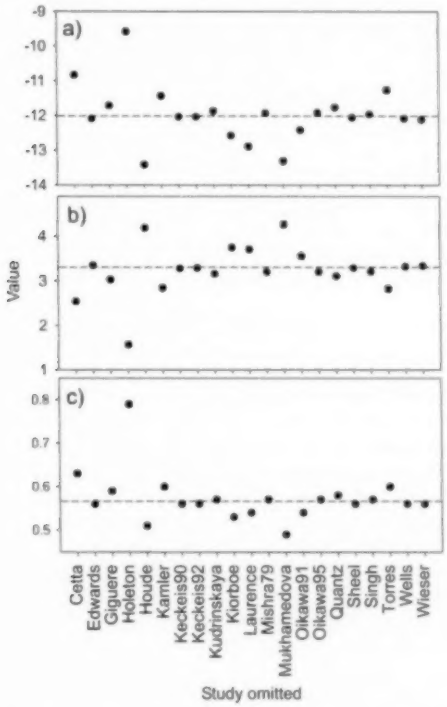
Fig. 9. Sensitivity of (*a*) parameter *A*, (*b*) parameter *B*, and (*c*) parameter *C* to author bias. The parameters were reassessed excluding one author at a time. The broken lines indicate the parameter estimates based on the entire data series.



particular interest. The adjusted mean weight of larvae <1 mg in mass in our data series was 158 µg. An extrapolation of Winberg's (1960) model to fish of equivalent weight (dashed line in Fig. 10) fall within the 95% confidence limits and very close to the mean calculated from our data (Fig. 10). Interestingly, all freshwater species fall within the 95% confidence limits and all the outliers are marine species. We can only speculate on whether the higher variability in metabolic rates in marine fish larvae is due to a salinity effect.

While the general conformity of the extension of Winberg's (1960) model to the actual metabolic rates determined for larvae is comforting and suggests fundamental similarities in metabolism versus size at all sizes, some caution is called for, since extrapolation of Winberg's (1960) linear regression to the lower larval size ranges does not account for the changing mass exponent characteristic of the early stages of development. As our data show, a curvilinear model is more robust at these size ranges.

Is there a universal model of fish metabolism?

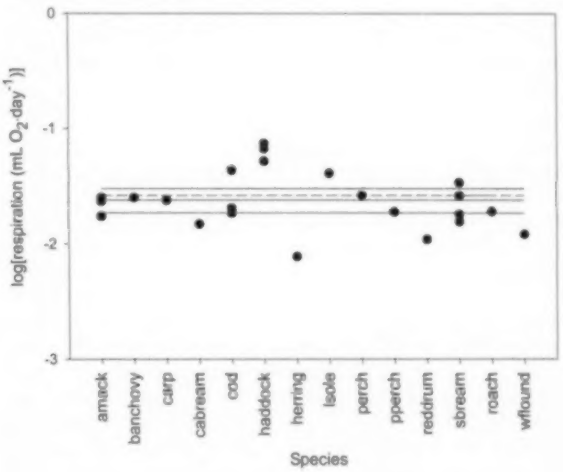
Both Winberg (1960) and Clarke and Johnston (1999) based their models on a fish size range within which the relationship between the logarithm of body weight and logarithm of respiration rates is linear. The slopes of their resulting regressions were essentially equal (0.81 and 0.80, respectively). These differ from the fundamentally non-linear relationships we describe for larval fishes where the mass exponent changes from 1 to 0.75 with fish weight (Fig. 3).

Table 3. Sample calculations for oxygen consumption using parameters derived for the whole data set (all data) and based on all data excluding Holeton's (1973, 1974) data with particularly strong influence (Fig. 9).

	Oxygen consumption (mL O_2·day^{-1})		
Dry weight (µg)	All data	Without Holeton	% change
10	0.0012	0.0014	+20
100	0.0147	0.0131	−12
1000 (1 mg)	0.112	0.095	−18
100 000	0.646	0.601	−7
1 000 000 (1 g)	13.16	18.48	+29

Note: The difference, however, can be entirely accounted for by temperature for these high-latitude fish living at −1.5 to 6°C.

Fig. 10. Respiration rates of larvae <1 mg by individual species. The extrapolation of Winberg's (1960) model (broken line) is close to the mean respiration rate for larvae of this size range and within the 95% confidence limits (solid lines). amack, Atlantic mackerel; banchovy, bay anchovy; cabream, carp bream; lsole, lined sole; pperch, pike perch; reddrum, red drum; sbream, sea bream; wflound, winter flounder.



We explored two questions: 1) how do the three independent data sets compare when transformed into equivalent units and 2) is there a general equation summarizing fish metabolism from larvae to adults which is consistent with the changing mass exponent during ontogeny?

Applying the conversions outlined in the Materials and methods, Winberg's (1960) formula becomes

(7) $\log R$ (mL·day^{-1}) = −3.36 + 0.81 log dw (µg)

where R is oxygen consumption and dw is dry weight. We multiplied the equation in Clarke and Johnston (1999) by 2 to convert standard to routine metabolism. Their model becomes

(8) $\log R$ (mL·day^{-1}) = −3.5 + 0.80 log dw (µg)

How well do these equations conform to our data for larval fish? From Fig. 3, we know that the slope of metabolism versus body weight decreases from 1 (i.e., isometry) to ap-

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proximately 0.75. However, an extension of the linear regression in Fig. 3 would lead to unrealistically low mass exponents, which means that an asymptotic relationship needs to be found that reflects an invariant mass exponent at larger body sizes. Let us assume that the total time required for consumption of a certain volume of oxygen is the time required for inherent cell metabolism plus the time required for transport of oxygen from gills to tissue. The time for delivery of a particular amount of oxygen is the inverse of its rate so that

$$(9) \qquad \frac{1}{R} = \frac{1}{R_1} + \frac{1}{R_2}$$

where R is the total respiration rate and R_1 and R_2 are the rate of metabolism and the rate of transport, respectively (U. Borgmann, Environment Canada, National Water Research Institute, Burlington, ON L7R 4A6, Canada, personal communication). We should expect that the inherent cell metabolism scales as a function of weight and therefore with an exponent of 1:

$$(10) \qquad \log R_1 = a + \log \text{dw}$$

The rate of transport of blood through the cross-sectional area in blood vessels, however, may be scaling according to the surface to volume ratio (two thirds rule; but see Kleiber 1961):

$$(11) \qquad \log R_2 = b + 0.67 \log \text{dw}$$

In small fish, R_1 will dominate; in larger fish with longer distances between gills and the receiving tissue, R_2 will be the limiting rate. Substituting eqs. 10 and 11 for R_1 and R_2, we arrive at the final equation:

$$(12) \qquad \log R = \log\left(\frac{1}{\frac{1}{10^{(a+\log \text{dw})}} + \frac{1}{10^{(b+0.67\log \text{dw})}}}\right)$$

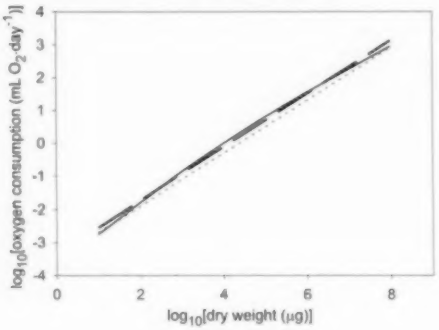
The slope at any point of log dw is the first derivative of eq. 12:

$$(13) \qquad \text{Slope} = \frac{10^{(b+0.67\log \text{dw})} + 10^{(a+\log \text{dw})} \times 0.67}{10^{(a+\log \text{dw})} + 10^{(b+0.67\log \text{dw})}}$$

We next applied eq. 13 to our data using the data set shown in Fig. 3 and the least squares Gauss–Newton method to obtain the two parameters $a = -3.71$ and $b = -2.40$ (Fig. 3).

The resulting relationship between metabolism and size for larval fish (eq. 12) together with Winberg's (1960) and Clarke and Johnston's (1999) models are shown in Fig. 11 (note that Winberg (1960) and Clarke and Johnston (1999) have been extrapolated to overlap the range of our data series). The strong coherence of the three independent data sets over a broad range of size and across many species and studies suggests that a common relationship indeed exists (Fig. 11). Even the slight discrepancy between the Winberg (1960) and Clarke and Johnston (1999) models is readily accounted for by their use of different temperature conversions. This coherence confirms Winberg's (1960) original hypothesis of a general equation describing fish metabolism.

Fig. 11. General model for larval and juvenile metabolism developed in this study (solid line, eq. 12) and its position relative to extrapolations of the models of Winberg (1960) (broken line) and Clarke and Johnston (1999) (dotted line).



We conclude that Winberg's (1960) linear function can be extended to include larval size ranges for a first approximation. It is important to note, however, to fully account for the changing mass exponent at the larval stage, the curvilinear model (eq. 12 with $a = -3.71$ and $b = -2.40$) may be a more accurate representation of the true relationship. Plotting data evenly along the general eq. 12 in a size range from 10 to 10^8 µg (i.e., the entire range of our data) and using a linear least squares regression results in a slope of 0.81, identical to that of Winberg (1960). Given the typical scatter of biological data, this curvature is very subtle and can easily be overlooked. However, eq. 12 must be treated with caution outside its domain because of its asymptote at 0.67 instead of the more commonly observed mass exponents of 0.75–0.79, which are the result of a more complex set of adaptations (Kleiber 1961; Peters 1983; Goolish 1995).

In conclusion, the finding that a single metabolic rate model can be applied to the full size range of fishes has implications for future studies of respiration in fish. Any one of the models displayed in Fig. 11 will provide a useful first approximation to fish metabolism in relation to size. Caution should be exercised, however, when applying these models to individual fish species. A great deal of important biological information is hidden in the scatter of the data around the relationships reported. This presumably results from individual variability, activity levels, and evolutionary adaptations to differing environments. Departures from these general equations may therefore reveal interesting and as yet undiscovered biological features. No doubt, improvements in experimental and measurement protocols will also reveal that a portion of the variance in the existing data is due to experimental error. We conclude that Winberg's (1960) hypothesis has been confirmed by 40 years of independent, high-quality work. The convergence of three large, independent data sets is no coincidence, and it is unlikely that the parameters of the general equation would change markedly by simply adding more data. While the general relationship does not necessarily provide an accurate prediction of respiration rates of individual fish, it provides a standard for comparisons among fish species and across classes and phyla. Its most important potential is to provide a baseline

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for the development of new hypotheses on the biology, ecology, and evolution of fish species.

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Guidelines for these contribution types are available from the Editorial Office's web site <http://www.uoguelph.ca/~cfas/>.

The publication process

Submit manuscripts in triplicate to the Editors, *Canadian Journal of Fisheries and Aquatic Sciences*, University of Guelph, Department of Zoology, Building #006, Room 107, Guelph, ON N1G 2W1, Canada, accompanied by a covering letter that (1) states the main points and significance of the work, (2) avows that all coauthors fully participated in and accept responsibility for the work, (3) avows that the manuscript is not being considered for publication elsewhere, (4) suggests potential referees, (5) identifies other manuscripts, including "extended abstracts," containing the same, similar, or related information, and (6) includes the telephone and fax numbers, as well as e-mail and current mailing addresses of all authors. Original typescripts and figures (except halftones) are best retained by the author until requested. Enclose the manuscript text, tables, and figures on diskette, specifying the software package(s) and version(s) used; Microsoft Word is the preferred word processing package for **review purposes**. **Packaging of manuscripts and illustrations should be robust enough to resist damage in transit.**

Each manuscript is normally submitted to two referees for appraisal, before final evaluation by the Editors and (or) Associate Editors. However, the Editors will return unreviewed those manuscripts that do not fall within the Journal's scope or character, and those that exceed the Journal's guidelines for prior publication as "extended abstracts" (guidelines available from the Editorial Office's web site). Papers submitted for inclusion in Journal Supplements are treated with the same rigor of review as articles in regular issues.

As general guidelines: manuscripts should not exceed 36 double-spaced pages, inclusive of references, tables, and figures; the number of references should not normally exceed 36; the number of tables plus figures should not normally exceed 12. Shorter, efficiently written papers are encouraged. Longer Articles (e.g., with more tables and figures) and longer Perspectives (e.g., with more references) will certainly be accepted, provided that their significance and interpretation of the new knowledge are commensurate with their length.

Responses to referees and revisions to manuscripts should normally be completed within 90 days. Manuscripts not returned within 90 days of receipt may be treated as new submissions unless the authors contact the Editorial Office.

Copyright material—Whenever a manuscript contains material that is protected by copyright (aerial photographs, figures, tables, etc.), it is the obligation of the author to secure **written permission from the holder of the copyright** to reproduce the material **for both the print and electronic formats**. These letters must accompany the submitted manuscript; otherwise, publication may be delayed. All material designated as "taken from..." must be accompanied by a letter of permission. If the material is not to be reproduced exactly as in the original, it should be designated as "modified from..." In either case the source of the material must be included in the reference list.

Submission of final accepted manuscript—Authors are requested to submit the **final accepted manuscript only, both in hard copy format and on disk**. Text files and figure files should be submitted on separate disks. All disks must be labeled clearly with the authors' names. **Text** (including tables) should be provided in a word-processing format (any form of

Aussi disponible en français

WordPerfect, Microsoft Word, or TeX is preferable, IBM compatible or Macintosh). TeX macros for preparing papers for submissions are available at <ftp://ftp.tex.ac.uk/tex-archive/macros/latex/contrib/supported/nrc/>, <ftp://ftp.dante.de/tex-archive/macros/latex/contrib/supported/nrc/>, and <ftp://ctan.tug.org/tex-archive/macros/latex/contrib/supported/nrc/>. Identify the word-processing software, version number, and type of computer used (IBM or Macintosh). For **figures**, see the section "Preparation of Electronic Illustration Files." Include a statement in the letter accompanying the manuscript that the version on the disk exactly matches the final hard copy version.

Galley proofs—A galley proof, illustration proofs, the copy-edited manuscript, and a reprint order form are sent to the corresponding author. **Galley proofs must be checked very carefully, as they will not be proofread by NRC Research Press**, and must returned within 48 h of receipt. The proof stage is not the time to make extensive corrections, additions, or deletions. The cost of changes introduced at the proof stage by the author, if deemed to be excessive, will be charged to the author.

Reprints—If reprints are desired, the reprint order form must be filled out completely and returned with payment (cheque, credit card number, purchase order number, or journal voucher) together with the corrected proofs and manuscript. Orders submitted after the Journal has been printed are subject to considerably higher prices. **The Journal does not provide free reprints and reprints are not mailed until a purchase order number or payment is received.**

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Requests for permission to republish the paper, in whole or in part, should be sent to NRC Research Press.

Preparation of manuscripts

General guidelines

Movement of manuscripts through review channels and the Editorial Office is greatly expedited if manuscripts are prepared in Journal style and format. General guidelines follow.

Type the manuscript on white paper (21.6 × 27.9 cm (8.5 × 11 in.)) on only one side of the page. Leave all margins at least 2.5 cm (1 in.) wide. Type only the title, authors' names and affiliations, and related footnotes on the first page. Number all pages beginning with the title page, including those for tables and captions for illustrations. **Double-space all parts of the manuscript**, including tables, captions for tables and figures, footnotes, and the reference list. Use italic font if available; when not available, underline material that is to be set in italics. Do not use all capitals anywhere in the manuscript. Use the name-and-year system for literature citations.

Editorial practices

Spelling should follow that of *Webster's Third New International Dictionary* or the *Oxford English Dictionary*. Authors are responsible for consistency in spelling.

The *CBE Manual for Authors, Editors, and Publishers: Scientific Style and Format* (6th ed., 1994) published by the Council of Biology Editors, Inc., Chicago, IL 60603, U.S.A., is used as the authority in matters of form. Titles of periodicals are abbreviated as in *BIOSIS Serial Sources* (BIOSIS, 2100 Arch Street, Philadelphia, PA 19103-1399, U.S.A.). Authors are responsible for ensuring the accuracy and completeness of their reference list. The Journal follows the names and spelling for fishes recommended in *A List of Common and Scientific Names of Fishes from the United States and Canada* (5th ed., 1991, Spec. Publ. No. 20, American Fisheries Society) and the gene nomenclature for protein-coding loci outlined in Shaklee et al. (1990, Trans. Am. Fish. Soc. **119**: 2–15). **SI** units (Système international d'unités) should be used or SI equivalents should be given. This system is explained and other useful information is given in the *Canadian Metric Practice Guide* (1989) published by the Canadian Standards Association (178 Rexdale Blvd., Etobicoke, ON M6N 3T3, Canada). For practical reasons, some exceptions to SI units are allowed (noted in the editorial in the Journal, Vol. 40, No. 12).

Checklist for manuscripts

Attention to the following questions will expedite appraisal of manuscripts by referees and editors.

Are the findings, interpretations, and conclusions adequately documented and relevant to the purpose of the study?

Are all the tables and figures needed and organized to facilitate comparison? Are there inconsistencies between tables and figures and the text, or within the text? Should some of the data be made available separately in a data or manuscript report or at a data depository?

If statistical analysis is included, is it subordinate to the research? When probability statements are made, are only the statistical tests cited and unnecessary statistical tables excluded?

Would any of the text be clearer if condensed? Are summary statements given at the beginning of sections and paragraphs, and are details in sections and paragraphs relevant to their topics? Does the organization of the manuscript follow logically from the statement of purpose in the introduction?

Does the **title** encompass the content of the report? Does the Abstract give the essentials of the new knowledge? Is the **Introduction** largely limited to the scope, purpose, and rationale of the study? Is review of the literature limited to defining the problem? Are details of **Materials and methods** limited to what readers need to understand the design of the study and to judge the adequacy of the data? Are generalizations from the **Results** supported by the data provided? Are findings distinguished from inferences? Is the **Discussion** limited to interpretation and significance of the findings?

The most common technical problems in submitted manuscripts are listed below. Authors can hasten the processing of their papers if they pay attention to these points during manuscript preparation.

(1) Limit abstract to one paragraph of about 175 words.
(2) Double-space all elements of the manuscript, including references, table captions, and figure legends.
(3) Avoid exclusive use of capitals anywhere in the manuscript, including headings, table captions, and figure legends.
(4) Italicize only Latin names of organisms and appropriate statistical and mathematical notations.
(5) Use correct SI symbols for units or measure in figures, tables, and text. Place a zero before the decimal for numbers less than unity.
(6) Avoid ambiguous forms such as g C/m^2/day; use g C·m^{-2}·day^{-1}.
(7) Identify the test used to test statistical significance and give the probability value. No reference is needed for common statistical tests.
(8) In the text, generalize from tables and figures; avoid re-

peating all the details. Be sure each table and figure can stand on its own and is referred to in the text in numerical order. The captions should explain the purpose of the table or figure.

(9) Include an acknowledgement section at manuscript stage, not when page proofs arrive.

(10) Provide the person's initials and mailing address when referring to personal communications.

(11) Delete unnecessary references that do not apply directly to the problem.

(12) Check references carefully against text citations and vice versa to ensure exact correspondence. Provide an availability statement for less easily retrieved material, e.g., available from Department of Economics, Simon Fraser University, Burnaby, BC V5A 1S6, Canada.

(13) Delete commas between name and date in citations such as (Smith 1990) and do not underline or italicize "et al."

(14) Replace 10^n in table headings and figure axes with appropriate SI prefixes or use words (e.g., thousands).

(15) Photocopies of figures, except halftones, are appropriate for review purposes. Send photographic prints, laser printouts, or original artwork/electronic files of figures (see "Illustrations" and "Preparation of electronic illustration files") on request for publication. Use the same type of lettering throughout if possible.

Parts of the manuscript

Organization

Organize the manuscript on the basis of the purpose or scope of the study as stated in the introduction. Ensure that the title and headings are in harmony with the statement of purpose.

Before writing any of the manuscript, list tentative headings in as few ranks as possible. Rework them until they appear to allow logical development for the reader; usually, chronological order is not effective. The findings will be more readily appreciated if methods, findings, and discussion are given in separate sections.

Organize tables and figures to facilitate comparisons, grouping related data in as few tables and figures as feasible. As far as possible, make the tables and figures clear without reference to the text.

Begin sections and paragraphs with topic sentences containing generalizations that lead readily to the particulars. Giving a conclusion first and then supporting it not only improves readability but also facilitates assessment by other scientists. Failure to give the most newsworthy generalizations first is one of the most prominent shortcomings in presentation of manuscripts.

See that everything in each section is relevant to the heading, and everything in each paragraph to the topic (opening) sentence.

Before writing any paragraphs, try writing the topic sentences for all of them and arranging these in appropriate order.

Title

Limit the title to what is documented in the manuscript. It is the key to the article and should clearly and concisely reveal what appears in the paper itself. The title serves two functions: (1) it allows the reader to judge whether or not the article is of potential interest and (2) it should provide enough information to permit the reader to judge the scope and potential importance of the article. Words in the title should convey a maximal amount of information and identify the nature of the research, organism used, and where appropriate, the technical approach (e.g., X ray, chromatography, mathematical analysis). Titles should not begin with a numeral or introductory prepositions such as "On" or "Towards" or expressions such as "A contribution to..." or "Investigations on..." Good titles greatly assist scientists and librarians in using scientific literature and aid indexers in preparing titles for keyword indexes. Series titles should be avoided.

Abstract

An abstract is required for all manuscripts and should state concisely, in up to 175 words, what was done, found, and concluded. Like the title, the abstract enables readers to determine the paper's content and decide whether or not they need to read the entire article. Begin the abstract with the main conclusion from the study, and support it with the relevant findings. Limit details of methods to those needed in understanding what was done, and work them into statements of findings. Avoid using phrases such as "...is discussed" or "...was found"; be specific. As the abstract is often divorced from the main body of the paper by abstracting and indexing services and is the only part of a paper some readers ever see, it is important that it accurately reflect the paper's contents and be completely self-contained (i.e., any *essential* references) in a retrievable form (e.g., R.B. Deriso. 1980. Can. J. Fish. Aquat. Sci. **37**: 268–282).

Introduction

Limit the introduction largely to the scope, purpose, and rationale of the study. Restrict the literature review and other background information to that needed in defining the problem or setting the work in perspective. Try beginning with the purpose or scope of the work, defining the problem next, and adding guideposts to orient the reader. An introduction generally need not exceed 375–500 words.

Materials and methods

Materials and methods provides the framework for getting answers to the questions posed in the purpose of the work.

Limit the information on materials and methods to what is needed in judging whether the findings are valid. To facilitate assessment, give all the information in one section when possible. Refer to the literature concerning descriptions of equipment or techniques already published, detailing only adaptations. Often, it helps to begin statements on procedures with a phrase indicating the purpose, such as "To determine...we..." If the section is long, consider using subheadings corresponding to headings for the findings.

Results

Limit the results to answers to the questions posed in the purpose of the work, and condense them as comprehensively as possible. Give the findings as nearly as possible in the terms in which the observations or measurements were made and so avoid confusion between facts and inferences. State noteworthy findings to be noted in each table and figure, and avoid restating in the text what is clear from the captions. Material supplementary to the text can be archived in the report literature or a recognized data depository and referenced in the text.

Discussion

Limit the discussion to giving the main contributions of the study and interpreting particular findings, comparing them with those of other workers. Emphasis should be maintained on synthesis and interpretation and exposition of broadly applicable

generalizations and principles. If these are exceptions or unsettled points, note them and show how the findings agree or contrast with previously published work. Limit speculation to what can be supported with reasonable evidence. End the discussion with a short summary of the significance of the work and conclusions drawn. If the discussion is brief and straightforward, it can be combined with the results section.

Acknowledgements

We strongly urge authors to limit acknowledgments to those who contributed substantially to scientific and technical aspects of the paper, gave financial support, or improved the quality of the presentation. Avoid acknowledging those whose contribution was clerical only.

References

References should be selected judiciously and be largely restricted to significant, published literature. References to unpublished data, manuscripts in preparation or submitted to other journals, progress reports, and unpublished papers given at annual meetings may not be cited in the reference list but may be noted in the text as unpublished data or personal communications (include mailing addresses). If consultants' reports or other documents of limited circulation must be cited, they should carry with them an availability statement explaining where the document can be obtained. **Citations of literature in the text should be carefully checked against those in the reference list and vice versa to ensure exact correspondence.** Nearly every manuscript submitted to the Journal contains errors in the references.

Footnotes

Footnotes to material in the text should not be used unless they are unavoidable, but their use is encouraged in tables. Where used in the text, footnotes should be cited in the manuscript by superscript Arabic numbers (except in the tables, see below) and should be numbered serially beginning with any that appear on the title page. Each footnote should be typed on the manuscript page on which the reference to it is made; **footnotes should not be included in the list of references**.

Equations

Equations should be clearly typed; triple-spacing should be used if superscripts and (or) subscripts are involved. Superscripts and subscripts should be legible and carefully placed. Distinguish between lowercase *l* and the numeral *one*, and between capital *O* and the numeral *zero*. A letter or symbol should represent only one entity and be used consistently throughout the paper. Each variable must be defined in the text, or in a **List of symbols** to appear after the reference list. Variables representing vectors, matrices, vector matrices, and tensors must be clearly identified. Numbers identifying equations must be in parentheses and placed flush with the **left margin**. In numbering, no distinction is made between mathematical and chemical equations.

Tables

Tables are used to present repetitive data and should be as economical of space as possible. Design tables to fit a 1-, 1½-, or 2-column width of the Journal. Type each on a separate page and number with Arabic numerals. Use horizontal lines above and below the headings and below the columns, and seldom elsewhere. Never use vertical lines; leave extra space instead. Table captions should be succinct and identify the purpose of the table sufficiently well to allow the table to stand on its own. Indicate table footnotes by superscript lowercase letters and type them below the table. Place the tables after the list of references. Note that *text tables* are not numbered, are typed within the text, and seldom need horizontal lines.

Appendices

Figures and tables used in an appendix should be numbered sequentially but separately from those used in the main body of the paper, for example, Fig. A1, Table A1, etc.

Supplemental material

The National Research Council of Canada maintains a depository in which supplementary material may be placed, either at the request of the author or suggestion of the Editors. Such material may include extensive tables of data, detailed calculations, and maps not essential for understanding and evaluating the paper. Such material must be clearly marked when the manuscript is submitted. Tables and figures should be numbered in sequence separate from those published with the paper (e.g., Fig. D1, Table D1). The supplemental material should be referred to by footnotes. Copies of material in the depository may be purchased from the Depository of Unpublished Data, CISTI, National Research Council of Canada, Ottawa, ON K1A 0S2, Canada.

Illustrations

Provide photographic reproductions, laser printouts, or the original artwork (no larger than 27.9 × 43.2 cm (11 × 17 in.)) of each illustration. Provide three sets of illustrations for review purposes.

Each figure or group of figures should be planned to fit, after appropriate reduction, into the area of either one or two columns of text. The maximum finished size of a one-column illustration is 8.8 × 23.9 cm (3.5 × 9.4 in.) and that of a two-column illustration is 18.2 × 23.9 cm (7.2 × 9.4 in.). The figures (including halftones) must be numbered consecutively in Arabic numerals, and each one must be referred to in the text and must be self-explanatory. All terms, abbreviations, and symbols must correspond with those in the text. Only essential labelling should be used, with detailed information given in the caption. Each illustration must be identified by the figure number and the authors' names on the back of the page or in the left-hand corner, well away from the illustration area.

Line drawings should be made with black ink or computer-generated in black on high-quality white paper or other comparable material. For computer-generated graphics, supply a laser print at the highest resolution available. **Photocopies are not acceptable.**

All lines must be sufficiently thick (0.5 points minimum) to reproduce well, and all symbols, superscripts, subscripts, and decimal points must be in good proportion to the rest of the drawing and large enough to allow for any necessary reduction without loss of detail. Avoid small open symbols; these tend to fill in upon reproduction. **Lettering produced by dot matrix printers or typewriters, or by hand, is not acceptable.** The same font style and lettering sizes should be used for all figures of similar size in any one paper.

Maps must have very clear, bold patterns and must show longitudes and latitudes (or UTM coordinates) and a scale. All place names and geographic features on Quebec maps must be in French only, with proper accents and capitalization.

Photographs should be *continuous tone* on glossy paper. Prints must be of high quality, on glossy paper, with strong contrast. The copies for reproduction should only show essential features, be trimmed, and mounted on **thin** flexible white bristol board with no space between those arranged in groups. A photograph, or group of them, should be planned to fit into the area of either one or two columns of text **with no further reduction**. Electron micrographs or photomicrographs should include a scale bar directly on the print. The best results will be obtained if the authors match the contrast and density of all figures arranged as a single plate.

Color illustrations will be at the author's expense. Further details on prices are available from Cecily Pearson, Managing Editor of the Journal (613-993-9099; fax: 613-952-7656; e-mail: cecily.pearson@nrc.ca).

NRC Research Press prefers the submission of electronic illustration files for accepted manuscripts and will use these electronic files whenever possible. If electronic files are not available, paper versions of the figures will be scanned. Note that the scanner will easily reproduce flaws (e.g., correction fluid, smudges). Submission of noncontinuous (screened) photographs and scanned illustrations printed out on laser printers is not recommended as moirés develop; a moiré is a noticeable, unwanted pattern generated by rescanning or rescreening an illustration that already contains a dot pattern.

Preparation of electronic illustration files

Authors must supply copies of the original electronic files (i.e., the files directly from the software application that they were created in) and **high-quality laser proofs** of the images. **Electronic files (i.e., figure number and figure content) should match the laser proofs.** On the disk label, identify (1) the software application and version; (2) file name(s), size, and extension; and (3) if the files have been imported from another software. If you have compressed your files, indicate what compression format was used. PC or Macintosh versions of True Type or Type 1 fonts should be used. **Do not use bitmap or nonstandard fonts.** Electronic graphics can be accepted on the following disks: 3½-in. disks, 100-MB Zip cartridge, and CD-ROM.

All figures should be submitted at their final published size. For figures with several parts (e.g., *a*, *b*, *c*, *d*, etc.) created using the same software application, assemble them into one file rather than sending several files.

Remember that the more complex your artwork becomes, the greater the possibility for problems at output time. Avoid complicated textures and shadings, especially in vector illustration programs; this increases the chance for a poor-quality final product.

Bitmap (raster) files—Bitmaps are image files produced using a grid format in which each square (or pixel) is set to one level of black, colour, or grey. A bitmap (rasterized) file is broken down into the number of pixels or picture elements per inch (ppi). Pixels per inch is sometimes referred to as dots per inch (dpi). The higher the resolution of an image, the larger the number of pixels contained within the rectangular grid.

The proper resolution should be used when submitting bitmap artwork. The minimum requirements for resolution are 600 dpi for line art and finelines (line art with fine lines or shading), 300 dpi for halftones and colour, and 600 dpi for combinations (halftones with lettering outside the photo area).

All *colour* files submitted must be as CMYK (cyan, magenta, yellow, and black). These colours are used in full-colour commerical printing. RGB graphics (red, green, and blue; colours specifically used to produce an image on a monitor) will not print correctly.

Vector files—Vector files are image files produced using elements such as lines and shapes. Typically these files are used for *line drawings*.

Bitmaps inside vector files—Bitmaps can be imported into vector/draw applications only for the purpose of adding and overlaying information, lines, text, etc. Bitmaps should not be resized, cropped, rotated, or otherwise manipulated after importing.

The preferred graphic application of NRC Research Press is CorelDraw! For other applications that can be used, see the "Electronic graphics list" at <http://www.nrc.ca/cgi-bin/cisti/journals/rp/rp2_prog_e?cjfas_graphics_e.html>.

Format conventions

Abbreviations

Abbreviate terms denoting units of weight and measurement in the text only when they are preceded by numerals.

becquerel (Bq)
calorie (cal)
centimetre (cm)
centimetre, square (cm^2)
centimetre, cubic (cm^3)
centimetres per gram per second ($cm \cdot g^{-1} \cdot s^{-1}$)
coulomb (C)
decimetre (dm)
degree Celcius (°C)
degrees of freedom (df)
gram (g)
hectare (ha)
hertz (Hz)
hour (h)
joule (J)
kilometre (km)
litre (L)
lumen (lm)
lux (lx)
metre (m)
metre, square (m^2)
metre, cubic (m^3)
micrometre (μm)
milligram (mg)
millilitre (mL)
millimetre (mm)
millimetre, square (mm^2)
minute (min)
molar mass (M)
mole (mol)
moles per litre (mol/L, M)
Pascal (Pa)
second (s)
standard deviation (SD)
standard error (SE)
tonne (metric ton) (t)
volt (V)
volume (vol)
watt (W)

Dates

Dates may be written in the sequence day–month–year without internal punctuation (On 9 October 1983 the...), or the alternative sequence month–day–year may be used with the year offset by commas (On October 9, 1983, the...).

Reference citations in text

Name-and-year system

The Journal uses the name-and-year system of citation; that is, the surname of the author(s) and the year of publication are inserted in the text at an appropriate point: "Brown (1983) compared..." or "...were compared (Brown 1983)." If the reference has more than two authors, include only the surname of the first author followed by "et al." (not italicized): "Brown et al. (1983) compared..." or "...were compared (Brown et al. 1983)."

Personal communications

Personal communications are not listed in the reference list. Using parentheses in the text, state the name and mailing address of the communicator followed by "personal communication."

Unpublished data

If an unpublished book or article has been accepted for publication, list it in the reference list section followed by the notation "In press." Only those manuscripts that are in galley or page proof stage or for which there is an acceptance letter can be considered in press. If an article is submitted but not yet accepted, state the name and address of the author of the unpublished material

followed by the notation "unpublished data" in the text and do not include it in the reference list.

Reference lists

References should be listed at the end of the paper in alphabetical order according to surnames of the first author. References with the same first author are listed in the following order. (1) Papers with **one author only** are listed first in chronological order, beginning with the earliest paper. (2) Papers with **dual authorship** follow and are listed in alphabetical order by the last name of the second author. (3) Papers with **three or more authors** appear after the dual-authored papers and are arranged chronologically.

The following bibliographic citations illustrate the punctuation, style, and abbreviations (according to *CASSI* or *BIOSIS Serial Sources*) for references.

Journal article

Peterman, R.M. 1982. Model of salmon age structure and its use in preseason forecasting and studies of marine survival. Can. J. Fish. Aquat. Sci. **39**: 1444–1452.

Entire issue of journal

Gordon, D.C., Jr., and Hourston, A.S. (*Editors*). 1983. Proceedings of the Symposium on the Dynamics of Turbid Coastal Environments. Can. J. Fish. Aquat. Sci. **40**(Suppl. 1).

Book in a series

Scott, W.B., and Crossman, E.J. 1973. Freshwater fishes of Canada. Bull. Fish. Res. Board Can. No. 184.

Book not in a series

LeBlond, P.H., and Mysak, L.A. 1978. Waves in the ocean. Elsevier, New York.

Part of book

Healey, M.C. 1980. The ecology of juvenile salmon in Georgia Strait, Britsh Columbia. *In* Salmonid ecosystems of the North Pacific. *Edited by* W.J. Neil and D.C. Himsworth. Oregon State University Press, Corvallis, Oreg. pp. 203–229.

Corporate author

American Public Health Association, American Water Works Association, and Water Pollution Control Federation. 1975. Standard methods for the examination of water and wastewater. 14th ed. Washington, D.C.

Theses

Kutty, M.N. 1999. Some studies on the respiratory quotient in goldfish and rainbow trout. Ph.D. thesis, University of Toronto, Toronto, Ont. Natl. Libr. Can., Can. Theses Microfilm No. 646.

Reports

Smith, J.E. 1981. Catch and efforts statistics of the Canadian groundfish fishery on the Pacific coast in 1980. Can. Tech. Rep. Fish. Aquat. Sci. No. 1032.

Translation

Koike, A., and Ogura, B. 1977. Selectivity of meshes and entrances of shrimp traps and crab traps. J. Tokyo Univ. Fish. **64**: 1–11. (Translated from Japanese by Can. Transl. Fish. Aquat. Sci. 4950, 1983.)

Time

A colon should be used as the separator between hour and minute and between minute and second. The symbols "h," "min," and "s" are not used because they are symbols for hour, minute, and second in the sense of duration or the length of time. Thus, "12 h 30 min" expresses a measured time of twelve hours and thirty minutes duration whereas 12:30 refers to the time of day.

Word list

The spelling of the following words is frequently inconsistent in submitted manuscripts. We prefer that authors adhere to the Journal's house style for these commonly used terms:

age-class (n.)
aquaculture (n.)
Arctic char (n.)
brackish water (n.)
brackish-water (adj.)
cold water (n.)
cold-water (adj.)
deep sea (n.)
deep-sea (adj.)
deep water (n.)
deepwater (adj.)
freshwater (n., adj.)
fresh water (n.)
groundwater (n., adj.)
hard water (n.)
hardwater (adj.)
headwater (n., adj.)
lake water (n., adj.)
meltwater (n., adj.)
open water (n.)
open-water (adj.)
percent (n.)
salt water (n.)
saltwater (adj.)
sea-run (adj.)
seawater (n., adj.)
shallow water (n.)
shallow-water (adj.)
size-class (n.)
snowmelt (n.)
soft water (n.)
softwater (adj.)
tidewater (n., adj.)
t test (n., adj.)
warm water (n.)
warmwater (adj.)
year-class (n.)
young-of-the-year (n., adj.)

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Recommandations aux auteurs

Journal canadien des sciences halieutiques et aquatiques

La Rédaction encourage la soumission d'articles contribuant à l'enrichissement des connaissances des sciences halieutiques et aquatiques. Les articles peuvent porter sur les cellules, les organismes, les populations, les communautés, les écosystèmes ou les procédés qui affectent les systèmes aquatiques. Ils peuvent traiter de disciplines variées y compris la biologie et l'écologie des organismes d'eau douce et d'eau salée, la limnologie, l'océanographie, la physiologie, la toxicologie, la génétique, l'économie, les maladies et la gestion. Les articles sont choisis selon la portée et l'importance des nouvelles connaissances ou idées qu'ils contiennent. On accorde la préséance aux articles qui contribuent à la compréhension de phénomènes observés et à l'interprétation de résultats expérimentaux.

Nous invitons les auteurs à soumettre des articles ayant des objectifs précis ou relevant des hypothèses, concepts ou questions vérifiables et se terminant par de solides conclusions ou d'utiles synthèses. Ces articles enrichissent, changent, mettent en question ou réorientent les connaissances acquises sur divers aspects des sciences aquatiques. La raison d'être de l'analyse et l'interprétation des résultats doivent être situées dans un vaste contexte disciplinaire ou interdisciplinaire. Les articles de méthodologie et de modélisation doivent inclure des applications et prouver la supériorité de la méthodologie ou du modèle explicité.

La Rédaction décourage la soumission d'articles simplement descriptifs (à moins qu'il ne s'agisse de nouvelles disciplines), d'application très limitée (applicable à une seule année, une seule région ou un seul taxon, portant sur un unique composé chimique, etc.); d'articles qui ne font que reprendre les principes énoncés dans des articles précédents; et d'articles rendant compte de l'application de normes sans gain de méthodologie. Les études préliminaires ou fragmentaires, ou dont la pertinence à grande échelle n'est pas démontrée, et les interprétations purement spéculatives sont carrément rejetées.

Les articles doivent être aussi complets que possible. S'il est impossible d'inclure toute les données pertinentes dans un seul article, l'auteur devra inclure des renvois à des articles connexes et soumettre ceux-ci avec son propre article.

Le Journal publie le genre de textes suivants :

Articles—Études de vaste portée qui constituent de nouvelles contributions à la science.

Perspectives—Synthèses, critiques ou réévaluations de concepts ou de paradigmes couramment admis.

Discussions—Commentaire ou réponse sur des sujets récemment abordés dans le Journal.

Communications rapides—Présentations de nouveaux concepts, descriptions de nouvelles méthodologies ou courts textes sur des sujets d'actualité ou controversés.

On peut obtenir les caractéristiques précises de chacun de ces genres sur le site web du Bureau de la rédaction <http://www.uoguelph.ca/~cjfas/>.

Processus de publication

Les manuscrits (**en triple**) doivent être soumis aux directeurs scientifiques, *Journal canadien des sciences halieutiques et aquatiques*, University of Guelph, Département de zoologie, Édifice 006, bureau 107, Guelph, ON N1G 2W1, Canada, et accompagnés d'une lettre qui fait état (1) des principaux points et de l'importance du travail, (2) de la participation de tous les auteurs au manuscrit et de leur approbation de ce dernier, (3) de l'assurance que le manuscrit en question n'est pas en cours d'examen aux fins de publication dans une autre revue, (4) de suggestions quant aux arbitres éventuels, (5) des autres manuscrits, y compris de résumés étoffes contenant une information identique ou similaire à celle contenue dans le manuscrit soumis et (6) des numéros de téléphone et de télécopieur ainsi que du courriel et de l'adresse au courant de chaque auteur. L'auteur devra, de préférence, conserver les originaux du texte dactylographié et des figures (sauf les demi-teintes) jusqu'à ce qu'on les lui demande. Veuillez inclure le texte, les tableaux et les figures du manuscrit sur disquette, en précisant le(s) progiciel(s) et la (les) version(s) utilisés; le logiciel de traitement de textes préférés est Microsoft Word pour **l'examen par les réviseurs**. **Les manuscrits et les illustrations doivent être solidement emballés afin d'être protégés lors de l'expédition.**

Chaque article est habituellement soumis à une évaluation par au moins deux réviseurs avant d'être examiné par les directeurs scientifiques ou les directeurs scientifiques associés. Toutefois, les directeurs scientifiques renverront sans les évaluer tout article qui ne reflète pas la portée ou le caractère du Journal et les articles qui débordent des limites imposées pour la publication sous forme de « résumés approfondis ». On obtiendra les directives à cet égard sur le site web du Bureau de la rédaction. Les articles soumis aux fins de publication dans un supplément sont soumis au même rigoureux exercice d'examen que les articles des numéros réguliers.

Voici quelques recommandations générales. Les articles ne doivent pas compter plus de 36 pages dactylographiées à double interligne, y compris les références, les tableaux et les figures. L'auteur devrait limiter le nombre de références à 36 et le nombre combiné de tableaux et d'illustrations à 12. Nous encourageons la soumission d'articles brefs, de style clair. Nous accepterons d'examiner les articles plus longs (p. ex. comptant plus de tableaux et de figures que la norme) et les perspectives intensément étayées (c.-à-d. comptant beaucoup de références) pour autant que leur importance et leur interprétation de nouvelles connaissances en justifient la longueur.

On demande habituellement aux auteurs d'examiner les commentaires des réviseurs et de modifier leur texte en conséquence en 90 jours, tout au plus. Faute de respecter ce délai, l'article renvoyé par l'auteur sera traité comme une nouvelle soumission à moins que l'auteur n'ait au préalable dûment communiqué avec le Bureau de la rédaction.

Droits de reproduction—Lorsqu'un article contient de la documentation (tableaux, figures, schémas, etc.) déjà publiée, il incombe à l'auteur d'obtenir **une permission écrite du titulaire de ces droits d'auteur** pour permettre la reproduction de l'information **en format imprimé et électronique**. La lettre d'autorisation doit accompagner le manuscrit soumis, sans quoi le processus de publication pourra être retardé. Cette lettre sera exigée avec toute mention du type « Tirée de... ». Si une illustration est modifiée, de sorte qu'une telle autorisation

n'est pas requise, la formulation doit être explicite : « Modifiée d'après... ». Si l'illustration est reconstituée à partir d'informations tirées d'autres auteurs la mention doit être du même type que pour une référence.

Soumission de la version approuvée—Les auteurs sont priés de soumettre **une copie imprimée ainsi qu'une copie sur disquette de la version approuvée de l'article seulement**. Les fichiers de texte et les fichiers d'illustrations devront être soumis sur des disquettes distinctes. Le nom des auteurs doit être indiqué clairement sur chaque disquette soumise. Le **texte** (y compris les tableaux) devrait être soumis en format de traitement de texte (WordPerfect, Microsoft Word ou TeX est préférable, compatible à IBM ou Macintosh). Les macros en TeX et la documentation pour la préparation des soumissions sont maintenant disponibles à <ftp://ftp.tex.ac.uk/tex-archive/macros/latex/contrib/supported/nrc/>, <ftp://ftp.dante.de/tex-archive/macros/latex/supported/nrc/> et <ftp://ctan.tug.org/tex-archive/macros/latex/contrib/supported/nrc/>. Il importe d'indiquer le logiciel de traitement de texte utilisé, la version, de même que le type d'ordinateur (IBM ou Macintosh). En ce qui a trait aux **illustrations**, il convient de se reporter à la section « Préparation des fichiers électroniques des illustrations ». Tout article devra être accompagné d'une lettre faisant foi du fait que la version du texte sur disquette reflète exactement la version imprimée soumise.

Épreuves en placard—Une épreuve en placard, des épreuves des illustrations, une copie de l'article corrigé et un bon de commande de tirés à part sont envoyés à l'auteur correspondant. **Les épreuves en placard doivent être relues attentivement car elles ne sont pas corrigées par les Presses scientifiques du CNRC.** Elles doivent en outre être retournées dans les 48 h suivant leur réception. Au stade des épreuves, il n'est plus temps d'apporter des modifications importantes ni de faire des ajouts ou des suppressions. Les frais occasionnés par des modifications excessives devront être assumés par les auteurs.

Tirés à part—Pour obtenir des tirés à part, il est nécessaire de remplir le bon de commande à cet effet et de le retourner avec le paiement (chèque, numéro de carte de crédit, numéro du bon d'achat ou pièce de journal interne) en même temps que les épreuves et l'article corrigés. Le tarif des tirés à part commandés après la parution du numéro du Journal est fortement majoré. **Le Journal n'offre pas de tirés à part gratuits; ceux-ci ne sont postés qu'après réception d'un numéro du bon d'achat ou du paiement.**

Transfert des droits d'auteur—Tous les auteurs doivent compléter un formulaire de transfert des droits d'auteur au CNRC. On obtiendra ces formulaires auprès du directeur scientifique, dans tout récent numéro du Journal ou sur le site web des Presses scientifiques du CNRC.

Toute **permission de republication** partielle ou intégrale d'un article doit être obtenue auprès des Presses scientifiques du CNRC <http://www.nrc.ca/cisti/journals/>.

Préparation des manuscrits

Directives générales

Le processus de publication sera grandement facilité si les articles sont préparés conformément au style du Journal.

Dactylographiez le manuscrit sur papier blanc (21,6 sur 27,9 cm (8,5 sur 11 po)) sur un côté de la page. Laissez toujours une marge d'au moins 2,5 cm (1 po). Sur la première page, dactylographiez le titre, les noms et affiliations des auteurs et les renvois qui s'y rapportent. Numérotez toutes les pages, à commencer par la page-titre, de même que celles contenant les tableaux et les légendes des illustrations. Tout le manu- scrit, y compris tableaux, légendes des tableaux et des figures, renvois et liste de références, doit être dactylographié à **double interligne**. Si on ne dispose pas d'une police d'italique, souligner les passages à imprimer en italique. En aucun endroit du manu- scrit n'écrivez entièrement en majuscules. Pour les références citées dans le texte, utilisez le système nom et année.

Dispositions générales

L'orthographe doit suivre *Le Grand Robert*. Les accents doivent être insérés sur les majuscules. Les auteurs sont responsables de l'uniformité de l'orthographe.

Le *CBE Manual for Authors, Editors, and Publishers : Scientific Style and Format* (6e éd., 1994, Council of Biology Editors, Inc., Chicago, IL 60603, É.-U.) sert de guide quant à la forme de la présentation. Les titres de périodiques sont abrégés suivant *BIOSIS Serial Sources* (BIOSIS, 2100 rue Arch, Philadelphia, PA 19103-1399, É.-U.). C'est la responsabilité des auteurs de s'assurer que leurs références sont complètes et exactes. Pour les noms de poissons et leur orthographe, le Journal suit les recommandations contenues dans *A List of Common and Scientific Names of Fishes from the United States and Canada* (5e éd., 1991, Spec. Publ. No. 20, American Fisheries Society). Pour la nomenclature génétique pour les locus de codage des protéines, le Journal suit les recommandations contenues dans Shaklee et al. (1990, Trans. Am. Fish. Soc. **119** : 2–15). Il est recommandé de se servir du **Système international d'unités** ou, tout au moins, de fournir les équivalences en unités SI. Ce système est décrit dans le *Guide de familiarisation au système métrique*, publié en 1989 par l'Association canadienne de normalisation (178, boulevard Rexdale, Etobicoke, ON M6N 3T3, Canada). Pour des raisons pratiques, on permet certaines exceptions à l'utilisation du Système international d'unités (comme dans un éditorial du Journal, vol. 40, no 12).

Liste de contrôle pour manuscrits

Une attention particulière aux questions suivantes facilitera l'évaluation des manuscrits par les arbitres et les rédacteurs :

Les découvertes, interprétations et conclusions sont-elles bien documentées et pertinentes aux buts de l'étude?

Les tableaux et figures sont-ils tous nécessaires et agencés pour faciliter les comparaisons? Y a-t-il contradiction entre les tableaux ou les figures et le texte, ou à l'intérieur du texte? Est-ce que certaines données devraient être présentées séparément dans un rapport manuscrit ou dans un dépôt de données?

Si une analyse statistique est effectuée, la statistique cède-t-elle le pas à la recherche? Dans des énoncés de probabilité, les tableaux statistiques inutiles sont-ils exclus et seulement les tests statistiques cités?

Le texte gagnerait-il en clarté s'il était plus condensé, en tout ou en partie? Contient-il des exposés sommaires au début de chaque section ou paragraphe, et les détails de ces sections et paragraphes sont-ils pertinents au sujet traité? La marche du manuscrit est-elle conforme à la logique énoncée dans l'introduction?

Le **titre** est-il représentatif du contenu du rapport? Le **Résumé** donne-t-il l'essentiel des connaissances nouvelles? L'**Introduction** se limite-t-elle à une esquisse de la portée, du but et des raisons de l'étude? La revue de la littérature se limite-t-elle à la définition du problème? La section **Matériel et méthodes** contient-elle le minimum de détails qui permettront aux lecteurs de saisir les grandes lignes de l'étude et de juger de la valeur des données? Les généralisations sur les **Résultats** sont-elles adéquates? Permettent-elles de distinguer entre constatations et déductions? La **Discussion** est-elle limitée à l'interprétation et à l'évaluation des découvertes?

Sont énumérés, ci-dessous, des façons d'éviter les problèmes techniques les plus communs dans la soumission des manuscrits. En accordant une attention particulière à ces points lors de la préparation de leurs manuscrits, les auteurs peuvent accélérer le traitement des articles.

(1) Limiter le résumé à un paragraphe d'environ 175 mots.
(2) Dactylographier à double interligne tous les éléments du manuscrit, y compris la bibliographie et les légendes des tableaux et des figures.
(3) Éviter partout l'emploi exclusif de majuscules, y compris dans les en-têtes et les légendes des tableaux et des figures.
(4) Ne composer en italique que les noms latins

d'organismes et certaines notations statistiques et mathématiques qui devront être imprimés en italique.

(5) Dans les figures, les tableaux et le texte, exprimer les unités de mesure par leurs symboles SI propres. Pour les nombres inférieurs à l'unité, placer un zéro avant la virgule décimale.

(6) Éviter les formes ambiguës, telles que g C/m^2/jour; utiliser plutôt g C·m^{-2}·jour^{-1}.

(7) Identifier le test qui a servi à évaluer la signification statistique, donnant également la valeur de probabilité. S'il s'agit de tests communs, il n'est pas nécessaire d'en donner la référence.

(8) Dans le texte, généraliser à partir des tableaux et des figures; éviter une répétition de tous les détails. S'assurer que tous les tableaux et figures sont indépendants et mentionnés dans le texte dans l'ordre numérique. Les légendes doivent indiquer le but du tableau ou de la figure.

(9) Préparer la section des remerciements au stade du manuscrit et non à celui des épreuves.

(10) En référant à des communications personnelles, donner les initiales et l'adresse postale de la personne en cause.

(11) Éliminer toutes références qui ne s'appliquent pas directement au problème.

(12) Vérifier soigneusement la correspondance des références en regard des citations dans le texte et vice versa. Dans le cas de matériel difficilement accessible, indiquer l'endroit où le trouver (p. ex., disponible auprès du Département de biologie, Université Laval, Sainte-Foy, QC G1K 7P4, Canada).

(13) Éliminer les virgules entre le nom et la date dans les citations telles que (Smith 1990) et ne pas souligner ni mettre en italique et al.

(14) Dans les en-têtes de tableaux et sur les axes des figures, remplacer 10^n par les préfixes SI appropriés ou rédiger en toutes lettres (p. ex., milliers).

(15) Aux fins de la révision, les photocopies des figures, sauf pour les demi-teintes, sont appropriées. Sur demande, lorsqu'il s'agira de publier l'article, envoyer des photographies, des imprimés laser ou les dessins originaux/fichiers électroniques des figures (voir « Illustrations » et « Préparation des fichiers électroniques des illustrations »). Utiliser autant que possible un lettrage uniforme.

Parties du manuscrit

Organisation

Organiser le manuscrit par rapport au but ou à la portée de l'étude, tels qu'énoncés dans l'introduction. Il est particulièrement important que le titre et les sous-titres soient en harmonie avec les objectifs.

Avant de commencer la rédaction du manuscrit, dresser une liste provisoire des sous-titres ou en-têtes, avec le moins de divisions possible. Retoucher les jusqu'à ce qu'ils semblent assurer, pour le lecteur, une marche logique; ordinairement, l'ordre chronologique ne sera pas satisfaisant. Il sera plus facile d'évaluer les résultats si méthodes, résultats et discussion sont décrits dans des sections séparées.

Organiser les tableaux et les figures de façon à faciliter les comparaisons, groupant les données apparentées en aussi peu de tableaux et de figures que possible. S'assurer que ces derniers sont aussi clairs que possible sans référence au texte.

Commencer les sections et les paragraphes par des énoncés généraux qui aboutissent naturellement à des énoncés particuliers. Si la conclusion est donnée d'abord puis appuyée ensuite, non seulement le travail sera plus facile à lire, mais aussi les autres scientifiques pourront plus aisément en évaluer les résultats. Dans la rédaction des manuscrits, le défaut le plus commun est d'omettre de donner, au début, les généralités les plus dignes de mention.

Voir à ce que le matériel de chaque section soit pertinent à l'en-tête et que le matériel de chaque paragraphe se rapporte à la première phrase introduisant le sujet.

Avant de rédiger les paragraphes, composer la phrase thème de chaque paragraphe et disposer ces phrases dans l'ordre approprié.

Titre

Limiter le titre à ce que l'étude veut démontrer. C'est la clé de l'article et il devrait refléter clairement et brièvement le contenu de l'étude. Le titre a deux fonctions : (1) il permet au lecteur de juger si, oui ou non, l'article peut avoir un intérêt et (2) il devrait fournir suffisamment d'information pour permettre au lecteur de juger de la portée et de l'importance potentielle de l'article. Les mots du titre devraient fournir un maximum d'information et identifier la nature de la recherche, de l'organisme utilisé et, au besoin, la méthode d'approche technique (p. ex., rayons X, chromatographie, analyse mathématique). Les titres ne devraient pas commencer par un chiffre ou par des prépositions d'introduction telles que « Sur » ou « Vers », ou des expressions telles que « Contribution à… » ou « Recherche sur… ». De bons titres facilitent le classement des publications et leur utilisation par les scientifiques et les bibliothécaires. On évitera les titres en séries.

Résumé

Un résumé doit accompagner chaque texte et exposer brièvement, en 175 mots ou moins, ce qui a été fait, ce qui a été découvert et les conclusions auxquelles on est arrivé. Comme le titre, le résumé permet aux lecteurs de prendre connaissance du contenu de l'article et de décider si, oui ou non, il leur faut lire ce dernier en entier. Indiquer, au début du résumé, la principale conclusion de l'étude et l'appuyer par des découvertes pertinentes. Ne donner que les détails des méthodes nécessaires à la compréhension de ce qui a été fait et les insérer dans l'énoncé des découvertes. Éviter l'emploi de phrases telles que « … on y analyse » ou « … a été trouvé » ; être plus spécifique. Comme le résumé est souvent séparé du corps principal de l'article par les services d'analyse et de classement, c'est la seule partie d'un travail que certains lecteurs auront l'occasion de voir; il importe donc qu'il reflète précisément le contenu du travail et qu'il soit complet en lui-même (c.-à-d. les références absolument *essentielles* sont indiquées, sous forme retraçable, p. ex., R.B. Deriso. 1980. J. Can. Sci. Halieut. Aquat. **37** : 268–282).

Introduction

Limiter l'introduction à la portée, au but et à la raison de l'étude. Ne mentionner que les travaux publiés et autres informations nécessaires à la définition du problème et à la perspective du travail. Commencer avec le but ou la portée du travail, définir ensuite le problème et ajouter ici et là des jalons qui aideront à orienter le lecteur. En général, une introduction n'a pas besoin de dépasser 375–500 mots.

Matériel et méthodes

Cette section renferme ce dont on a besoin pour trouver réponse aux questions soulevées dans les objectifs du travail.

Limiter les renseignements à ce qui est nécessaire pour juger de la validité des découvertes. Cette évaluation sera facilitée si toute l'information est présentée, autant que possible, dans une section. S'il s'agit d'outillage ou de techniques déjà publiés, référer aux publications et ne décrire en détail que les adaptations. Il y a souvent avantage à commencer un énoncé des méthodes par une phrase qui en indique le but, comme : « Afin de déterminer… nous… ». Si la section est longue,

utiliser des sous-titres correspondant à ceux de la section des résultats.

Résultats

Limiter les résultats aux réponses apportées aux questions en rapport avec le but de l'étude; que ces réponses soient aussi complètes que possible, tout en étant concises. Exprimer, autant que possible, les découvertes dans les mêmes termes que les observations ou les mesures, évitant ainsi de confondre faits et spéculations. Dégager les généralités des tableaux et des figures et y référer en évitant de répéter dans le texte ce que les légendes devraient exprimer clairement. Le matériel complémentaire au texte peut être classé dans les séries de rapports ou dans un dépôt de données reconnu; et on y référera dans le texte.

Discussion

Limiter la discussion à l'énoncé de la principale contribution de l'étude et à l'interprétation de découvertes particulières, les comparant avec celles d'autres auteurs. On continuera à mettre l'accent sur la synthèse et l'interprétation, ainsi que sur l'exposition de généralisations et de principes largement applicables. S'il s'agit d'exceptions ou de points douteux, les noter et faire ressortir la manière dont les résultats corroborent ou contredisent les travaux déjà publiés. Limiter la spéculation à ce qui peut être appuyé sur des preuves raisonnables. Terminer cette section par un court résumé de l'importance du travail et des conclusions auxquelles il a conduit. Si la discussion est brève et précise, elle peut être combinée avec les résultats en une seule et même section.

Remerciements

Nous recommandons fortement aux auteurs de limiter les remerciements aux personnes qui ont contribué d'une manière substantielle aux aspects scientifiques et techniques de l'article, fourni une aide financière ou amélioré la qualité de la présentation. Éviter de mentionner les personnes qui n'ont fourni qu'un travail de soutien.

Références

On choisira les références avec soin, les limitant aux publications importantes. On ne peut citer dans cette section les références à des données inédites, manuscrits en préparation ou soumis à d'autres périodiques, états des travaux et communications inédites présentées à des réunions annuelles. On peut toutefois les mentionner dans le texte à titre de données inédites ou de communications personnelles (incluant les adresses). Si l'on doit citer des rapports d'experts-conseils ou d'autres documents dont la distribution est limitée, on devra préciser l'endroit où l'on peut se les procurer. **On doit s'assurer que les références mentionnées dans le texte correspondent à celles qui sont contenues dans la liste de références et vice versa.** Presque tous les manuscrits soumis au Journal contiennent des erreurs dans cette section.

Notes infrapaginales

Les notes infrapaginales ne devraient figurer dans le texte que lorsqu'elles sont inévitables, mais leur utilisation dans les tableaux est encouragée. Lorsque les notes infrapaginales figurent dans le texte, leurs appels devraient être désignés par des chiffres arabes en exposant (sauf dans le cas des tableaux, voir ci-dessous) et numérotés consécutivement à partir de la première note infrapaginale, y compris toute note apparaissant en page titre. Chaque note doit figurer au bas de la page où elle est signalée, **pas dans la bibliographie**.

Équations

Les équations doivent être dactylographiées clairement, à triple interligne si elles incluent des exposants ou des indices. Les exposants et les indices doivent être lisibles et correctement placés. Il convient de faire une distinction entre la lettre *l* et le chiffre *un*, et entre la lettre majuscule *O* et le chiffre *zéro*. Une lettre ou un symbole ne devrait représenter qu'une seule entité et devrait être utilisé de façon uniforme dans l'article. Chaque variable doit être définie dans le texte ou dans une **liste des symboles** devant apparaître après la bibliographie. Les variables représentant des vecteurs, des matrices, des matrices vectorielles et des tenseurs doivent être clairement définies. Les numéros d'équation doivent être identifiés par des chiffres arabes placés entre parenthèses et alignés avec la **marge de gauche**. Aucune distinction n'est faite entre la numérotation des formules mathématiques et celle des formules chimiques.

Tableaux

Les tableaux sont utilisés pour présenter des données qui se répètent et devraient occuper le moins d'espace possible. Agencez les tableaux de façon qu'ils s'adaptent soit à 1, 1½ ou 2 colonnes du Journal. Dactylographiez chaque tableau sur une page séparée et numérotez-les en chiffres arabes. Tracez des lignes horizontales de part et d'autre des en-têtes et au-dessous des colonnes, mais rarement ailleurs. N'utilisez jamais de lignes verticales. Laissez plutôt des espaces supplémentaires. Chaque tableau doit avoir une légende instructive, complète et indépendante. Les renvois des tableaux doivent être indiqués par des minuscules suscrites dactylographiées au bas du tableau. Placez les tableaux après la liste des références. Notez que les *tableaux dans le texte* ne sont pas numérotés et sont dactylographiés dans le corps du texte. Ils ont rarement besoin de lignes horizontales.

Annexes

Les illustration et les tableaux en annexe doivent être numérotés différemment des illustrations et tableaux du corps de l'article, p. ex. figure A1, tableau A1, etc.

Documentation complémentaire

Le Conseil national de recherches administre un Dépôt des données non publiées dans lequel la documentation complémentaire peut être versée, à la demande des auteurs ou du directeur scientifique. La documentation complémentaire peut comprendre de grands tableaux, des calculs complexes et des cartes détaillées qui ne sont pas essentiels à la compréhension ou à l'évaluation du document. Les auteurs qui désirent utiliser ce service doivent clairement indiquer les parties dont ils demandent le dépôt dès la soumission de leur article. Les tableaux et les figures doivent être numérotés de façon consécutive, distinctement de ceux destinés à la publication (p. ex. : figure D1, tableau D1). Toute donnée déposée doit faire l'objet d'une note infrapaginale à la section appropriée du document. Des copies des données déposées peuvent être obtenues contre paiement auprès du Dépôt des données non publiées, ICIST, Conseil national de recherches du Canada, Ottawa, ON, K1A 0S2, Canada.

Illustrations

Fournir des photographies, des imprimés laser (les imprimés par imprimante par points sont inacceptables) ou les dessins originaux (pourvu qu'ils ne dépassent pas 27,9 sur 43,2 cm (11 sur 17 po)) de chaque illustration. Transmettre trois copies des illustrations qui serviront au moment de la révision.

Chaque figure ou groupe de figures doit être préparé de manière à occuper, après une réduction appropriée, l'espace d'une ou deux colonnes du texte. Les dimensions finies maximales d'une illustration sur une colonne sont de 8,8 sur 23,9 cm (3,5 sur 9,4 po) et celles d'une illustration sur deux colonnes est de 18,2 sur 23,9 cm (7,2 sur 9,4 po). Les figures (y

compris les similigravures) sont numérotées en chiffres arabes selon leur ordre séquentiel et doivent être annoncées dans le texte bien que tous leurs éléments doivent être intelligibles en eux-mêmes. Tous les termes, les abréviations et les symboles qui se trouvent dans les figures doivent être les mêmes que ceux apparaissant dans le texte. Seuls les détails essentiels devraient être identifiés; l'information plus détaillée devrait paraître dans la légende. Chaque illustration doit être identifiée, de préférence au bas, à gauche, par le numéro de la figure et les noms des auteurs, suffisamment éloignés de l'espace réservé à l'illustration.

Les **dessins au trait** originaux doivent être en encre noire ou produits par ordinateur en encre noire sur du papier blanc de première qualité ou un matériau comparable. Quant aux graphiques produits par ordinateur, il faut fournir un imprimé au laser de la meilleure résolution disponible. **Les photocopies ne sont pas acceptables.**

L'épaisseur des lignes doit être suffisante (au moins 0,5 point) pour que la reproduction soit nette; tous les symboles, les indices supérieurs ou inférieurs et les signes décimaux doivent être en bonne proportion avec le reste du dessin et suffisamment marqués pour permettre la réduction nécessaire sans perte de détail. Ne pas utiliser de petits symboles ouverts qui ont tendance à se refermer lorsqu'ils sont reproduits. **Le lettrage produit par imprimante à matrice de point ou par machine à écrire, ou à la main, ne sont pas acceptables.** Le même style de police et la même dimension de lettrage doivent servir dans toutes les figures de dimensions semblables d'un article.

Les **cartes** doivent avoir des motifs clairs et gras, et comporter les longitudes et latitudes (ou les coordonnées de Mercator transverses universelles) de même qu'une échelle graphique. Tous les noms d'endroits et les caractéristiques géographiques sur les cartes du Québec doivent être en français seulement, avec les accents et les majuscules appropriés.

Les **photographies** doivent être en demi-teintes sur papier glacé. Les épreuves doivent être de première qualité, sur papier glacé, avec contrastes bien marqués. Les copies destinées à la reprographie doivent être rognées de façon à ne laisser paraître que les éléments essentiels et être montées sur carton bristol blanc **léger** et flexible. Aucun espace ne doit paraître entre les photographies constituant une même planche. Une photographie ou un groupe de photographies doit être préparé de manière à occuper, **sans réduction supplémentaire**, une ou deux colonnes du texte. Les micrographies électroniques et les photomicrographies doivent comporter une échelle graphique à même l'illustration. On évitera les pertes de détails et de contraste inhérentes au procédé d'imprimerie en agençant le contraste et la densité de toutes les photographies montées sur une même planche.

Les **illustration en couleurs** sont aux frais de l'auteur. On peut obtenir de plus amples renseignements sur les prix auprès de Cecily Pearson, rédactrice administrative du Journal (613-993-9099; télécopieur : 613-952-7656; courriel : cecily.pearson@nrc.ca).

Les Presses scientifiques du CNRC préfèrent recevoir la version électronique des illustrations des manuscrits acceptés et l'utiliseront dans la mesure du possible. Si les fichiers électroniques ne sont pas disponibles, la version papier des illustrations sera balayée. Toutefois, le lecteur optique reproduit facilement les défauts (p. ex., le liquide correcteur, les maculations). Il est recommandé de ne pas soumettre de photographies tramées, ni des illustrations balayées imprimées au laser, à cause des moirures qui se forment; une moirure est un motif perceptible et non désiré produit par le rebalayage ou le retramage d'une illustration qui contient déjà un motif de points.

Préparation des fichiers électroniques des illustrations

Les auteurs doivent fournir des copies des fichiers électroniques originaux (c.-à-d. les fichiers tirés directement du logiciel sur lequel ils ont été créés) et des **épreuves au laser de haute qualité** des images. **Les fichiers électroniques (c-à-d. le numéro et le contenu de la figure) doivent correspondre aux épreuves au laser.** Sur l'étiquette de la disquette, il faut indiquer (1) l'application et la version du logiciel; (2) le(s) noms(s), la dimension et le suffixe du fichier; et (3) si les fichiers ont été importés d'un autre logiciel. Si les fichiers ont été comprimés, il faut indiquer le format de compression. Les versions PC ou Macintosh des polices True Type ou Type 1 doivent être utilisées. **On ne doit pas se servir des polices de caractères en mode points ou non standard.** Les graphiques électroniques sont acceptés sur les disquettes suivantes : disquettes 3½ po, cartouche Zip de 100 Mo et sur CD-ROM.

Toutes les illustrations doivent être soumises dans leur dimension de tirage final. Quant aux figures comportant plusieurs parties (p. ex., *a*, *b*, *c*, *d*, etc.) crées sur le même logiciel, elles doivent être assemblées dans un seul fichier plutôt que de transmettre plusieurs fichiers.

Il faut **garder** les illustrations le plus simple possible afin d'éviter les embûches. Éviter les textures et les fonds grisés compliqués, particulièrement dans les programmes d'illustration vectorielle.

Fichier en mode point—Les fichiers d'images en mode point sont produits sur une grille dans laquelle chaque carré (ou pixel) correspond à une nuance de noir, de couleur ou de gris. Un fichier en mode point est défini par le nombre de pixels ou d'éléments par pouce. Comme le pixel est défini comme un point, on parle aussi de « points par pouce » ou « ppp ». Plus la résolution de l'image est grande, plus le nombre de points sur une surface donnée est élevé.

Les illustrations soumises en mode point doivent être de définition adéquate. Les exigences minimales de définition sont les suivantes : 600 ppp pour les dessins au trait et les lignes fines (les dessins au trait comportant des lignes fines ou un fond grisé), 300 ppp pour les demi-teintes et les couleurs et 600 ppp pour les combinaisons (demi-teintes avec lettrage à l'extérieur de l'espace réservé à la photo).

Tous les fichiers en *couleurs* soumis doivent suivre la base CMJK (cyan, magenta, jaune et noir). Ces couleurs sont utilisées dans l'impression commerciale tout en couleur. Les graphiques RVB (le rouge, le vert et le bleu sont les couleurs utilisées particulièrement pour produire les images sur un écran) ne s'impriment pas correctement.

Fichiers vectoriels—Les fichiers vectoriels sont des fichiers d'images composées d'éléments comme les lignes et les formes. Ce type de fichier convient habituellement aux *dessins au trait*.

Fichiers vectoriels en mode point—Le mode points peut être importé dans un logiciel vectoriel ou de dessins aux seules fins d'ajouter et de superposer de l'information, des lignes, du texte, etc. Le mode points ne doit pas être redimensionné, recadré, tourné ou manipulé de toute autre façon après avoir été importé.

Le logiciel graphique préféré par les Presses scientifiques du CNRC est CorelDraw! Pour les autres applications possibles, reportez-vous à la « Liste des programmes graphiques électroniques » à <http://www.nrc.ca/cgi-bin/cisti/journals/rp/rp2_prog_f?cjfas_graphics_f.html>.

Conventions

Abréviations

N'abréger les termes désignant les unités de poids et mesures dans le texte que lorsqu'ils sont précédés d'un nombre.

becquerel (Bq)
calorie (cal)
centimètre (cm)
centimètre carré (cm^2)
centimètre cube (cm^3)
centimètres par gramme par seconde ($cm \cdot g^{-1} \cdot s^{-1}$)
coulomb (C)
décimètre (dm)

degré Celsius (°C)
degrés de liberté (dl)
écart type (ET)
électronvolt (eV)
erreur type (ErT)
farad (F)
gramme (g)
hectare (ha)
hertz (Hz)
heure (h)
joule (J)
kilomètre (km)
litre (L)
lumen (lm)
lux (lx)
mètre (m)
mètre carré (m^2)
mètre cube (m^3)
micromètre (µm)
milligramme (mg)
millilitre (mL)
millimètre (mm)
millimètre carré (mm^2)
minute (min)
masse molaire (M)
mole (mol)
moles par litre (mol/L, M)
pascal (Pa)
seconde (s)
tonne (métrique) (t)
volt (V)
volume (vol)
watt (W)

Dates

On écrira les dates dans l'ordre jour–mois–année, p. ex. 9 octobre 1983, sans virgule entre le mois et l'année.

Citations de références dans le texte

Système de nom et année

Le Journal utilise le système de nom et année, c.-à-d. que le nom de l'auteur ou des auteurs et l'année de publication sont insérés dans le texte à un endroit approprié : « Brown (1983) compare… » ou « …on a comparé (Brown 1983) ». Si la référence comporte plus de deux auteurs, inscrivez le nom du premier auteur seulement, suivi de « et al. » : « Brown et al. (1983) comparent… » ou « …on a comparé (Brown et al. 1983) ».

Communications personnelles

Les communications personnelles ne doivent pas être incluses dans la liste des références. Utilisez plutôt des parenthèses dans le texte, entre lesquelles vous indiquerez le nom et l'adresse de la personne en question, suivis de « communication personnelle ».

Données inédites

Si un livre ou un article inédit a été accepté pour publication, insérez-le dans la liste des références, avec la mention « Sous presse ». On ne peut considérer comme étant sous presse que les manuscrits au stade d'épreuves ou ceux couverts par lettre d'acceptation. Si un article a été soumis mais n'a pas encore été accepté, ne l'incluez pas dans la liste de références, mais indiquez le nom et l'adresse de l'auteur du matériel inédit, dans le texte lui-même, avec la mention « données inédites ».

Liste de références

Les références doivent être classées par ordre alphabétique des noms des premiers auteurs. Si la liste comprend plusieurs publications d'un même premier auteur, les règles suivantes seront appliquées. (1) S'il n'y a qu'**un auteur**, les ouvrages se succèdent par ordre chronologique de partition en commençant par le plus ancient. Si l'auteur a publié, au cours d'une année, plusieurs livres ou articles, on distinguera les références les unes des autres en faisant suivre l'année de publication d'une lettre (*a*, *b*, *c*, etc.). (2) S'il y a **deux auteurs**, les ouvrages sont placés à la suite de ceux n'ayant qu'un auteur, et sont alors classés par ordre alphabétique du nom du deuxième auteur. (3) S'il y a **trois auteurs ou plus**, les ouvrages sont placés à la suite de ceux ayant deux auteurs et sont classés par ordre chronologique.

La liste qui suit donne des exemples de ponctuation, de style et d'abréviations utilisés dans les références bibliographiques (d'après *CASSI* ou *BIOSIS Serial Sources*).

Article d'une revue

Archambault, D., et Bourget, E. 1983. Importance du régime de dénudation sur la structure et la succession des communautés intertidales de substrat rocheux en milieux subarctiques. J. Can. Sci. Halieutiques Aquat. **40** : 1278–1292.

Numéro complet d'une revue

Gordon, D.C., Jr., et Hourston, A.S. (*Éditeurs*). 1983. Proceedings of the Symposium on the Dynamics of Turbid Coastal Environments. J. Can. Sci. Halieutiques Aquat. **40**(suppl. 1).

Livre dans une série

Hilton, J.W., et Slinger, S.J. 1981. Nutrition et alimentation de la truite arc-en-ciel. J. Can. Sci. Halieutiques Aquat. publ. spéc. n° 55.

Livre ne faisant pas partie d'une série

Forrester, W.D. 1983. Manuel canadien des marées. Service hydrographique du Canada, ministère des Pêches et des Océans, Ottawa.

Partie d'un livre

Aubert, M., Aubert, J., Daniel, S., et Desirotte, N. 1982. État actuel de la pollution bactérienne au large des côtes françaises. *Dans* La pollution des mers et les ressources biologiques. *Éditeur* : M. Ruivo. Fishing News (Books) Ltd., London. pp. 36–40.

Corporation auteur

American Public Health Association, American Water Works Association et Water Pollution Control Federation. 1975. Standard methods for the examination of water and wastewater. 14e éd. Washington.

Thèse

Delisle, C. 1969. Écologie, croissance et comportement de l'éperlan du Lac Heney, Comté de Gatineau ainsi que la répartition en eau douce du Québec. Thèse de doctorat, Université d'Ottawa, Ottawa.

Rapport

Dutil, D.J., Fortin, M., et Vigneault, Y. 1982. L'importance des zones littorales pour les ressources halieutiques. Mémoire remis au Conseil consultatif de l'environnement du Québec. Rapp. Manuscrit Can. Sci. Halieutiques Aquat. n° 1653.

Traduction

Koike, A., et Ogura, B. 1977. Selectivity of meshes and entrances of shrimp traps and crab traps. J. Tokyo Univ. Fish. **64** : 1–11. (Traduit du japonais par Can. Transl. Fish. Aquat. Sci. 4950, 1983.)

Temps

On devra séparer par deux points (:) heures et minutes, et minutes et secondes. Les symboles « h, » « min » et « s » ne seront pas utilisés car ils représentent heure, minute et seconde dans le sens de durée ou intervalle de temps de douze heures et trente minutes, alors que 12 : 30 rapporte à l'heure du jour.

Liste de mots

Cette section, dans la version anglaise du Guide, contient une série de mots dont l'orthographe pose certains problèmes d'uniformité, comme, par exemple, « cold water » (n.) « cold-water » (adj.); « hard water » (n.) « hardwater » (adj.), etc. L'auteur préparant un texte en anglais est prié de consulter la version anglaise du Guide.

Presses scientifiques du CNRC
Conseil national de recherches du Canada
Ottawa, ON K1A 0R6
Canada

Télécopier : 613-952-7656
Courriel : research.journals@nrc.ca
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Révisé en janvier 2001

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Le titulaire peut être l'auteur, mais dans plusieurs cas, le titulaire est l'employeur de l'auteur:

13.(3) Lorsque l'auteur est employé par une autre personne en vertu d'un contrat de louage de service ou d'apprentissage, et que l'oeuvre est exécutée dans l'exercice de cet emploi, l'employeur est, à moins de stipulation contraire, le premier titulaire du droit d'auteur; mais lorsque l'oeuvre est un article ou un autre contribution, à un journal, à une revue ou à un périodique du même genre, l'auteur, en l'absence de convention contraire, est réputé posséder le droit d'interdire la publication de cette oeuvre ailleurs que dans un journal, une revue ou un périodique semblable.

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Les gouvernements, en particulier le gouvernement fédéral, ne disposent pas d'un mécanisme simple de cession de droit d'auteur pour ce genre de biens de la Couronne. C'est pourquoi lorsqu'un auteur est un fonctionnaire et que, par conséquent, le droit d'auteur appartient à la Couronne, une simple permission d'usage est suffisante pour l'éditeur, pour autant que celle-ci ait été octroyée par une personne jouissant de l'autorité nécessaire pour ce faire.

CALL FOR NOMINATIONS

HERZBERG MEMORIAL

Prize and Fellowship

Description

The Herzberg Memorial Prize and Fellowship was created in 1999 by the National Research Council of Canada (NRC), in commemoration of Gerhard Herzberg, renowned NRC scientist and Nobel laureate. It consists of a CAN$25,000 prize and a one-year fellowship tenable at one of NRC's institutes.

In addition to the Prize, the laureate receives compensation (the value of which is negotiable) for the tenure of the fellowship as well as for relocation and travel expenses.

Eligibility

The award is open to Canadian and foreign candidates. Nominees or applicants must be active researchers with many years of outstanding achievements in a field that is relevant to NRC's programs. They must also be committed to working for a period of approximately one year, on a full-time basis, in an NRC institute.

Nominations

Candidates may apply on their own behalf. They can also be nominated by their peers. In both cases, candidates must provide a curriculum vitae and a statement containing the following information:

- an outline of their major scientific achievements;
- the nature of the research activities they would like to pursue at NRC;
- their current research relationship, if any, with NRC; and
- the period of time during which they would be available to work at NRC.

Candidates applying on their own behalf should provide the names of at least three referees from whom NRC can solicit comments on a confidential basis. Nominations must be received by 28 February 2001.

To submit an application or to ask for additional information, please contact:

Serge Hamel, Corporate Services
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Building M-58, Montreal Road
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Tel.: (613) 993-3656
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APPEL DE CANDIDATURES

Prix et Bourse HERZBERG 2001

Description

Le Prix et la Bourse Herzberg ont été établis en 1999 par le Conseil national de recherches du Canada (CNRC) en mémoire de Gerhard Herzberg, chercheur émérite du CNRC et prix Nobel. Cette distinction comprend un prix de 25 000 $CAN ainsi qu'un stage d'environ un an dans un institut du CNRC. Une rétribution, dont le montant est négociable, est accordée pour le stage.

Admissibilité

Les candidats peuvent être du Canada ou d'autres pays. Ils doivent avoir à leur actif des réalisations exceptionnelles dans un domaine de recherche pertinent aux programmes du CNRC. Ils doivent aussi s'engager à travailler à temps plein dans un institut du CNRC pour une période d'environ un an.

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- un résumé de leurs principales réalisations scientifiques;
- la nature des activités de recherche qu'ils aimeraient poursuivre au CNRC;
- s'il y a lieu, leurs liens actuels ou récents avec le CNRC; et
- la période pendant laquelle ils seraient disponibles pour un stage au CNRC.

Les candidats qui posent eux-mêmes leur candidature doivent fournir les noms d'au moins trois personnes auxquelles le CNRC pourra demander des références en toute confidentialité.

Les candidatures doivent parvenir au CNRC au plus tard le 28 février 2001.

Pour soumettre des candidatures ou demander des renseignements supplémentaires, s'adresser à :

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